A STUDY OF GREEN CRAB (*CARCINUS MAENAS*) INTERACTIONS, CANNIBALISM, AND A FIRST APPROACH TO MODEL THE EFFECTS OF HARVESTING ON ITS POPULATIONS

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ABSTRACT

Green crabs (*Carcinus maenas*) have been extensively studied because of the negative impacts that they have on the ecosystems that they invade. However, there are still substantial gaps of knowledge about their interactions and population dynamics. As green crabs continue to invade new locations, it is important to gain a deeper understanding of these subject areas in order to prevent or mitigate further introductions or spread. This thesis aims to address these knowledge gaps by focusing on two main topics: (1) green crab predator-prey interactions with smaller conspecifics and a native counterpart, the mud crab (*Dyspanopeus sayi*), and (2) a first attempt using a model to predict green crab population dynamics and the potential effects of a removal program. First, I analysed long-term observational beach-seine data collected from the southern Gulf of St. Lawrence, and found that there was a negative association between native mud crabs and green crabs in this area. Then I used laboratory experiments to examine their predator-prey interactions and assessed the influence of habitat complexity on the outcome of these interactions. I found that green crab predators consumed almost twice as many mud crabs compared to juvenile green crabs in the two less structured habitats (no substrate or sandy substrate), but predation rates were statistically similar in oyster bed habitat. This study found that mud crab mortality was significantly affected by habitat type, whereas green crab mortality was not.

I then focused on green crab cannibalism by adults on juveniles with similar laboratory experiments. In this study, I included habitat types that represented a wider range of structural complexity, and found that cannibalism rates declined with

increasing habitat complexity. I also conducted field inclusion experiments that gathered similar results, though the differences were not significant.

I identified knowledge gaps and areas of future research by gathering all the available information about green crab life stages. This population information was used to build a relatively simple stage-based population matrix model for green crabs. The outcome of the model estimated that a theoretical green crab population could increase by approximately 43%. The outcome of this model also suggested that even if adult survival is set to zero (representing intensive trapping and effective removal of adults), the population was still able to grow because numbers in the other life stages were abundant enough to feed and maintain the population growth rate. These results suggests that current removal programs that catch mostly adults have little-to-no effect on the population growth rate, indicating that harvesting alone is unlikely to result in a reduction of annual green crab abundance.

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CHAPTER 1

General Introduction

1.1 Introduction

Invasive species are often colloquially described as the contents of a Pandora's Box because they are global problems that are often impossible to eradicate once they become established (Bax et al. 2003). Invasive species can have wide-reaching and sometimes devastating commercial and ecosystem-level scale impacts (Pimentel et al 2005). Marine invasive species, in particular, can spread quickly for a number of reasons. They are easily transported as larvae in ballast water of ships and have the potential to move far with ocean currents. Marine invasive species are able to thrive in their new invaded ranges, particularly those already disrupted by other causes, affecting native diversity and function. Once a marine invasive species becomes established in a new area, it is important to investigate mitigation strategies, its population dynamics, and examine its interactions with native species and various components of the ecosystem.

Green crabs (*Carcinus maenas* Linnaeus 1758) are listed among the top 100 worst invasive species (Lowe et al. 2000) due to the detrimental impacts that they have on invaded ecosystems. They are voracious predators that feed on many small bivalves and crustaceans, including younger stages of their own species (Baeta et al. 2006; Rossong et al. 2006; Breen and Metaxas 2008). For example, they have been associated with the decline of soft shelled clams (Grosholz et al. 2000), and are known to rip up and destroy eelgrass beds (*Zostera marina*), which are important nursery habitats for many marine organisms (Davis, Short, and Burdick 1998; Malyshev and Quijón 2011; Garbary et al. 2014). Green crabs were originally distributed along the eastern Atlantic coast of Europe

(Audet et al. 2003), but since the 1800s they have invaded many regions of the world. Today their distribution extends to areas of North and South America, South Africa, Australia, and Asia. Given their distribution and potential impacts, green crabs represent an interesting model species for the study of the life history and interactions of a marine invasive species.

On the East coast of North America, green crabs were first introduced in 1817 as larvae, arriving in the ballast water of ships (Audet et al. 2003). Since that time, they have expanded their range northward, with the aid of several additional introductions. In the Atlantic Canada region, they were found in the Bay of Fundy in the 1950s, first confirmed in Prince Edward Island (hereafter PEI) in 1997, and introduced to Newfoundland in 2007 (Audet et al. 2003; Blakeslee et al. 2010). Although green crabs have been extensively studied, there are still substantial gaps of knowledge about their population dynamics and interactions. As populations of this species continue to invade new locations, it is important to gain a deeper understanding of these subject areas in order to prevent or mitigate further introductions or spread.

This thesis addresses some of these knowledge gaps, by focusing on two main topics: (1) green crab predator-prey interactions with smaller conspecifics and a native species, and (2) the modelling of green crab population dynamics in the presence of a removal program. The thesis focuses first on the life history of this species with a comprehensive literature review of green crab population information. There is a lot of information about the different life stages of the green crab, but this information is scattered between publications and unpublished reports. In my literature review (Chapter 2), I summarized the available information about green crab fecundity and survival rates

between each of its life stages, longevity, and generation time. Such a summary was considered important and useful to support the development of a population model, and to identify green crab population dynamic knowledge gaps for further research.

Chapters 3 and 4 focus on better understanding how habitat variables affect green crab predation rates. Since green crabs reportedly impact the ecosystem that they invade, it is important to gain insight into how changes in habitat structure affect green crab predation rates. It is well established that higher habitat complexity decreases predation rates (Fernandez, Iribarne, and Armstrong 1993; Dittel, Epifanio, and Natunewicz 1996; Langellotto and Denno 2004; Stoner, Ottmar, and Haines 2010; Hill and Weissburg 2013), but this has not been explored in green crab predator-prey interactions.

Chapter 3 focuses on predator-prey interactions between green crabs and native mud crabs (*Dyspanopeus sayi*), an area of research which has not previously been explored. Since the range of mud crabs and green crabs overlap, both regionally and locally (within the intertidal zone; Breen and Metaxas 2009), I expect that these crabs are likely to interact in their environment. I used long term beach seine monitoring data from the southern Gulf of St. Lawrence to explore the temporal and spatial relationship between these two species. I then used 24 hour laboratory experiments using three different habitat mimics (no substrate, sandy sediments, and oyster bed mimic) to investigate how habitat complexity affects their predator-prey interactions.

Chapter 4 focuses on how habitat affects cannibalism rates between adults and juvenile size green crabs, a subject also unexplored to date. I conducted similar laboratory experiments to the ones used in Chapter 3, but testing five different types of habitat (no substrate, sandy sediments, mussel bed, oyster bed, mussel bed with sandy

sediments, and oyster bed with sandy sediments). In parallel, I also used field cage inclusion experiments with three habitat types (sandy sediments, mussel bed mimic with sandy sediments, and oyster bed mimic with sandy sediments). Although stomach content analyses of adult crabs have shown that cannibalism accounts for a small portion of the green crab's diet (Baeta et al. 2005; Chaves et al. 2010), most information available on green crab cannibalism is for newly-settled crabs (Moksnes 2004; Almeida et al. 2011), and no information was available about adult and juvenile cannibalism interactions.

Chapter 5 uses the information gathered in the literature review (Chapter 2) to feed a relatively simple population matrix model for green crabs. Since preventing new green crab introductions and stopping green crab range expansions is unlikely to be successful in most locations due to their dispersive larval life stage, it is more realistic to focus on potential mitigation measures. Harvesting green crabs via removal programs has been a common mitigation strategy. However many removal projects aiming to control green crab populations have been initiated without knowing whether removal efforts will have an actual impact on the population (e.g. Duncombe 2014; Therriault and Duncombe 2016; Matheson et al. 2016; Walton 2000; Klassen and Locke 2007). Chapter 5 presents a first attempt to develop a population matrix model that is expected to be useful in the understanding of the population dynamics of this species, and the exploration of removal strategies. I used this model to evaluate how each life stage contributes to the population growth and reproduction of green crabs, and to assess the impact of different removal strategies (harvesting programs) on the growth of the remaining population.

The last part of this thesis (Chapter 6) summarizes the main results of each of the data chapters, and makes recommendations for future research.

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CHAPTER 2

Green Crab (*Carcinus maenas*) Demography Literature Review

2.1 Introduction

Despite the economic and ecological importance of the green crab (*Carcinus maenas*), there are still substantial knowledge gaps about their population dynamics and interactions. Specifically, relatively little work has been carried out on population models aiming to understand their population dynamics and their application on control strategies. For this reason, I limited the scope of this literature review to a summary of green crab population dynamics, in order to assemble information required to build population models, like the one I developed in Chapter 5. Shorter literature reviews that focus on the green crab interactions and the effect of the habitat type on the outcome of those interactions can be found in the Introduction sections of Chapters 3 and 4.

Only one publication presents research that attempted to model some aspects of the invasion dynamics of green crab (Kanary et al. 2014), however more work could be done to assess removal strategies. The life history of green crabs suggests that stage-structured population models could be suitable for this species, as demonstrated for other crustaceans in the past (e.g. Miller 2001). However, the development of such models must rely on population dynamics/demography information that is currently scattered across the literature available.

Green crabs have five planktonic, larval stages (zoea 1-4, and megalopa) preceding a juvenile stage and then growing into a sexually mature adult. Here, I gathered all the available information about fecundity, survival rates between each of these stages, longevity, and generation time. Whenever the information was available, the effects of

temperature and salinity were reported for the different life history traits, and distinctions were made between data collected from the crab's native range and from invaded areas. I also provide an overview of green crab habitat use. This review also allowed me to identify knowledge gaps, and areas for future research.

2.2 Fecundity

In Europe, the fecundity of Green Crabs was estimated to be 185,000 - 200,000 eggs per brood under favourable conditions (Broekhaysen 1936 as cited by Cohen, Carlton, and Fountain 1995) whereas in areas like New Hampshire, natural variation in Green Crab fecundity is estimated at 75,577 ± 37,808 (Griffen 2014). On Prince Edward Island, Canada, fecundity was estimated at 195,833 ± 83.673 eggs/female at early development stages, and 140,374 ± 60,717 eggs/female at later development stages (developed eye pigments) (Audet, Miron, and Moriyasu 2008). See Table 2.1 for full summary of fecundity values.

Table 2.1: Fecundity estimates. Sources: 1: Broekhaysen (1936), as cited in many papers, including Cohen, Carlton, and Fountain (1995), 2: Aydin (2013), 3: Ozbek et al. (2012), 4: Griffen (2014), 5: Audet, Miron, and Moriyasu (2008).

	Fecundity estimate	Source	Sample size	Size of females studied	Comments
Native range	185,000 - 200,000	1	--	--	--
	272,162 ± 53,396	2	17	average CL=66mm	Estimate for similar crab species *Carcinus aestuarii*
	6000 - 126,969	3	--	average CL=28mm	
Invaded range	75,577 ± 37,808	4	16	--	--
	195,833 ± 83,673	5	14	CW = 41.5-68.30mm	Early development stages
	140,374 ± 60,717	5	19	CW = 41.5-68.30mm	With developed eye pigments

Green crabs have one brood per year in temperate waters (Audet, Miron, and Moriyasu 2008), whereas they may have up to two broods in warmer waters (Lovell, Besedin, and Grosholz 2007). A second brood could potentially double fecundity values, however this has not been investigated in the species, and a study on Red King Crab (*Paralithodes camtschaticus*), showed that lower temperatures in autumn led to decreased brood sizes compared to spring broods (Swiney et al. 2012).

Fecundity is affected by resource availability, female size, and temperature (Kennelly and Watkins 1994; Hines et al. 2004; Flores, Gomes, and Villano 2009). Griffen (2014) found that Green Crab fecundity increased by approximately 5,200 eggs when daily consumption of animal tissue increased by 1% of body weight. Audet, Miron, and Moriyasu (2008) found that the number of embryos increased with increasing abdomen width. Temperature is also thought to be an important factor in determining fecundity, though it is difficult to test experimentally.

Eggs are brooded externally by the female and hatch into plankton larvae after 17 - 80 days (Grosholz and Ruiz 2002). Laboratory experiments in England found that the hatching success rate was 0.71 – 0.85 at temperatures ranging between 11 and 24°C (maintained at normal sea water salinity), and 0.12 and 0.88 for salinities ranging from 17.4 - 43.5ppt (maintained at 24°C) (Hartnoll and Paul 1982). These data provide valuable estimates of survival rates from eggs to the zoea 1 larval stage. Berrill (1982) provided some data on the proportion of ovigerous females relative to all sexually mature females caught (based on their size) from June-August in Portugal (84 out of 335). However, this kind of data is likely biased due to the reduced feeding rates and

movement into deeper water that has been documented for ovigerous females (Ropes 1968).

2.3 Larval Stages

Several studies have observed green crabs develop through the larval stages in the laboratory and at different temperatures (4 - 25°C) (Dawirs 1985; Mohamedeen and Hartnoll 1989; Nagaraj 1993; deRivera et al. 2006). Experiments conducted in their native range found that the survival rates of green crab larvae ranged from zoea 1 to 1st crab instar range from 0.29 to 0.92 at temperatures between 12 and 25°C, and are summarized in Table 2.2 (Dawirs 1985; Mohamedeen and Hartnoll 1989). The range of survival rates from these studies is quite large. This variation could be an artifact of the small sample sizes, or a result of the difficulties and challenges with raising larvae in a laboratory setting, or it may be representative of the large variation in larval survival in the wild. I tried creating graphs and looked for trends in the data, but was unable to detect any patterns. deRivera et al. (2006) used individuals from both the West and East Coasts of North America (invaded range), and found that overall average survival peaked at 0.254 ± 0.066 at 17.5°C. They also reported survival rates (from zoea 1 to 1st crab instar) as a function of temperature:

Maine larvae: $Y = - 0.44 + 0.06X – 0.002X^2$
California larvae: $Y= -0.65 + 0.11X – 0.003X^2$

Nagaraj (1993) investigated the effects of different combinations of temperature (10 - 25°C) and salinity changes (20 - 35ppt). Using this data, they also created a model that can be used to predict percent mortality of each zoea l stage at different temperature-salinity combinations, and found that the highest survival under these conditions was at

10°C and 30 - 35ppt. Additionally, salinity tolerance was found to increase with each successive larval stage, meaning that survival rates in later larval stages extended to a wider salinity range than the early larval stages (Nagaraj 1993).

Many studies have reported data on the duration of larval development in a laboratory setting (from zoea 1 to 1st crab instar) ranging from 18.2 to 61.3 days (see Table 2.3 for data from various studies). It is clear from these data that larval duration increases with decreasing temperature, which is an important consideration for populations that live in waters that are <10°C for the majority of the year (Nagaraj 1993; deRivera et al. 2006). Additionally, larval development duration does not seem to be considerably affected by variations in salinity (Nagaraj 1993).

Table 2.2: Summary of larval survival rates from several studies. Data from Dawirs 1985 are taken from cumulative mortality for each stage. All studies were conducted in a laboratory environment in locations that are part of the green crab's native range. Letters in the temperature column represent different trials conducted at the same temperature.

Paper	Temp (°C)	Salinity (ppt)	Starting n	Zoea 1		Zoea 2		Zoea 3		Zoea 4		Megalopa		Survival from Zoea 1 to Megalopa	Overall survival from zoea 1 to 1st crab instar
				n	% Survival	n	% Survival	n	% Survival	n	% Survival	n	% Survival		
Nagaraj 1993	10	20	45	22	49%	17	77%	13	76%	5	38%			11%	
Nagaraj 1993	10	25	47	47	100%	33	70%	27	82%	22	81%			47%	
Nagaraj 1993	10	30	55	55	100%	51	93%	49	96%	47	96%			85%	
Nagaraj 1993	10	35	60	60	100%	57	95%	52	91%	44	85%			73%	
Dawirs 1985	12 A	31-33	25	25	100%	25	100%	24	96%	23	96%	22	96%	92%	88%
Dawirs 1985	12 B	31-33	25	24	96%	23	96%	23	100%	23	100%	19	83%	92%	76%
Dawirs 1985	12 C	31-33	50	49	98%	47	96%	45	96%	45	100%	27	60%	90%	54%
Dawirs 1985	12.5 A	31-33	50	49	98%	49	100%	48	98%	47	98%	46	98%	94%	92%
Nagaraj 1993	15	20	45	45	100%	27	60%	24	89%	16	67%			36%	
Nagaraj 1993	15	25	55	55	100%	42	76%	40	95%	32	80%			58%	
Nagaraj 1993	15	30	58	58	100%	55	95%	53	96%	47	89%			81%	
Nagaraj 1993	15	35	60	60	100%	50	83%	50	100%	43	86%			72%	
Mohamedeen and Hartnoll 1989	15 A	33-34	214	214	100%	196	92%	162	83%	132	81%	94	71%	62%	29%
Mohamedeen and Hartnoll 1989	15 B	33-34	120	120	100%	118	98%	110	93%	106	96%	104	98%	88%	35%
Dawirs 1985	18 A	31-33	25	20	80%	18	90%	18	100%	18	100%	17	94%	72%	68%
Dawirs 1985	18 B	31-33	25	25	100%	25	100%	25	100%	25	100%	16	64%	100%	64%

Dawirs 1985	18 C	31-33	50	43	86%	42	98%	42	100%	38	90%	31	82%	76%	62%
Dawirs 1985	18 D	31-33	50	49	98%	46	94%	46	100%	30	65%	9	30%	60%	18%
Paper	**Temp (°C)**	**Salinity (ppt)**	**Starting n**	**Zoea 1**		**Zoea 2**		**Zoea 3**		**Zoea 4**		**Megalopa**		**Survival from Zoea 1 to Megalopa**	**Overall survival from zoea 1 to 1st crab instar**
				n	% Survival	n	% Survival	n	% Survival	N	% Survival	n	% Survival		
Dawirs 1985	18 E	31-33	50	46	92%	46	100%	46	100%	44	96%	34	77%	88%	68%
Dawirs 1985	18 F	31-33	50	49	98%	48	98%	47	98%	45	96%	35	78%	90%	70%
Nagaraj 1993	20	20	51	51	100%	43	84%	33	77%	23	70%			45%	
Nagaraj 1993	20	25	52	52	100%	48	92%	44	92%	36	82%			69%	
Nagaraj 1993	20	30	45	39	87%	38	97%	37	97%	31	84%			69%	
Nagaraj 1993	20	35	51	51	100%	47	92%	46	98%	35	76%			69%	
Mohamedeen and Hartnoll 1989	20 A	33-34	140	140	100%	140	100%	140	100%	137	98%	130	95%	98%	58%
Mohamedeen and Hartnoll 1989	20 B	33-34	72	72	100%	72	100%	70	97%	67	96%	63	94%	93%	82%
Mohamedeen and Hartnoll 1989	20 C	33-34	48	48	100%	48	100%	47	98%	46	98%	43	93%	96%	83%
Nagaraj 1993	25	20	90	68	76%	60	88%	59	98%	37	63%			41%	
Nagaraj 1993	25	25	90	81	90%	57	70%	54	95%	51	94%			57%	
Nagaraj 1993	25	30	90	74	82%	56	76%	49	88%	43	88%			48%	
Nagaraj 1993	25	35	90	80	89%	65	81%	56	86%	44	79%			49%	
Dawirs 1985	25 A	31-33	50	42	84%	41	98%	40	98%	36	90%	26	72%	72%	52%

Table 2.3: Summary of larval development durations from various studies. All studies were conducted in a laboratory environment in locations that are part of the green crab's native range.

Paper	Temp (°C)	Salinity (ppt)	Larval development time (days)						
			zoea 1	zoea 2	zoea 3	zoea 4	megalopa	Zoea 1 - megalopa	**Total** (zoea 1 - 1st instar)
Dawirs 1986	9		20						
Nagaraj 1993	10	20	16.3	13.3	12.7	12.7		55	
Nagaraj 1993	10	25	12.8	11.3	12	14.5		50.6	
Nagaraj 1993	10	30	12.5	11.8	11.8	13		49.1	
Nagaraj 1993	10	35	14	12.3	11.8	15.3		53.4	51.9
Williams 1968 *	12	?	14.8	7.9	9.6	10	15.4	42.3	57.7
Dawirs 1986	12		8	8	8	10	21	34	55
Dawirs 1985	12		9.1	8.4	9.3	12	22.5	38.8	61.3
Dawirs 1985	12.5		7.2	6.5	7.2	9.6	17.6	30.5	48.1
Nagaraj 1993	15	20	11.5	10.8	12.3	12		46.6	
Nagaraj 1993	15	25	10.3	8.5	9.5	11.3		39.6	
Nagaraj 1993	15	30	9.5	7	9.5	12.3		38.3	
Nagaraj 1993	15	35	9	6.25	8	13.3		36.55	
Mohamadeen and Hartnoll 1989	15		5.3	5.7	6.6	8	14.7	25.6	40.3
Nagaraj 1993	20	20	8.5	8.5	9.3	11		37.3	
Nagaraj 1993	20	25	7	5.5	9.8	9.8		32.1	
Nagaraj 1993	20	30	5.5	6.3	8	13.3		33.1	
Nagaraj 1993	20	35	6.5	6.3	6.5	8.3		27.6	
Dawirs 1986	18		5	5	5	5	12	20	32
Dawirs 1982*	18	?	7.9	7.4	5.5	4	9.3	24.8	34.1
Dawirs 1982*	18	?	5.4	6.4	5.8	6.2	11.2	23.8	35
Dawirs 1985	18		4.7	4.1	4.2	5.8	12.9	18.8	31.7
Mohamadeen and Hartnoll 1989	20		3	3.4	4.2	5.1	9.6	15.7	25.6
Nagaraj 1993	25	20	6.6	5.7	5.3	6.7		24.3	
Nagaraj 1993	25	25	6.3	6.3	4.7	7.7		25	
Nagaraj 1993	25	30	6.7	6.7	5.7	5.7		24.8	
Nagaraj 1993	25	35	6.3	7	6	8		27.3	
Dawirs 1985	25		3.1	3.1	2.8	3.4	5.8	12.4	18.2
* as cited in Mohamedeen and Hartnoll (1989)									

2.4 Size and Age at Maturity, and Generation Time

In their native range, female green crabs reached the size of maturity at 21.5 - 44.9 mm CW, and males reached the size at maturity at 25 - 57.3 mm CW. In their introduced range, females reached the size of maturity at 30 - 47.7 mm CW, and males reached the size at maturity at 44.3 - 51.1 mm CW. Typically, introduced populations were larger than native populations (Klassen and Locke 2007; McGaw, Edgell, and Kaiser 2011). Age at maturity is between 1 - 3 years, which leads to a generation time between 2-4 years (see Table 2.4 for summary from different studies).

Table 2.4: Green crab carapace width (CW) measurements at sexual maturity.

	Source	Measurements at Sexual Maturity		
		Age	Female Size (mm)	Male Size (mm)
Native range	Lyons et al. (2012)	--	44.96	57.3
	Crothers (1967)*	--	15-31	25-30
	Eriksson and Edlund (1977)	2	--	--
	Eriksson and Edlund (1977)	1	--	--
	Broekhuysen 1936 ***	--	36-42	--
	d'Udekem d'Acoz 1993***	--	23-45	>44
	Almaza 1982***	--	21.5	27
	Mohamedeen and Hartnoll (1989)	--	27-49	--
Invaded range	Audet, Miron, and Moriyasu (2008)	--	36.9 - 43.79	44.32 - 49.48
	Sharp et al. (2003)	--	39.69 - 47.65	47.4 - 51.1
	Tremblay**	--	40-60	--
	Yamada and Hunt (2000) ****	<1	~30	--
	Behrens Yamada et al. (2005)	--	>32	--
	Berrill (1982)	2-3	>34	--

*as cited by Lyons et al. (2012); ** as cited by Klassen and Locke (2007); *** as cited in Audet, Miron, and Moriyasu (2008); **** as cited in Yamada et al. (2005).

2.5 Longevity and Adult Mortality

In the green crab's invaded range, longevity has been reported as 5 to 6 years in Maine, and 4 to 6 years in Oregon. Meanwhile, longevity has been reported as 3 to 4 years in their native range (Table 2.5). Natural mortality is quite difficult to estimate in crustaceans, and has been identified as the most important but least well-estimated parameter in fishery models (Vetter 1988). See Hewitt (2008) for an extensive overview of methods to estimate the natural mortality rate for crustaceans.

Table 2.5: Summary of green crab longevity estimates.

	Paper	Longevity
Native range	Baeta et al. (2005)	3-4
	Broekhuysen (1936)*	3-4
	Naylor (1962)*	3-4
Invaded range	Yamada et al. (2005)	4-6
	Berrill (1982)	5-6

*as cited in Baeta et al. (2005)

Mark-recapture studies are the most reliable, but are difficult for marine crustaceans because they are open populations and therefore there is often a lot of immigration/emigration. In addition, they do not retain any of their hard body parts when they molt. Edwards (1958) estimated green crab adult survival to be 0.64 – 0.88 from a mark-recapture study in England, but this was only for the month of August. Similarly, Munch-Petersen, Sparre, and Hoffmann (1982) estimated green crab adult survival to be 0.07 - 0.95 based on ten separate mark-recapture studies in Copenhagen, but each study only lasted 4 - 9 days and the authors acknowledge that these estimates are inaccurate due to the short time span of the experiment and the uncontrolled immigration/emigration. Natural mortality is likely much lower over the entire year.

Natural mortality can also be indirectly estimated using a linear regression model (Hoeing 1983) based on longevity, where *M* is the natural mortality, and t_{max} is the maximum possible age for the species (Hewitt 2008).

(1) $$\ln(M) = 1.44 - 0.982 * \ln(t_{max})$$

Assuming survival is the complement of mortality, equation 1 yields survival estimates of -0.435 – 0.273 based on the longevity estimates of 3 - 6 years (see above).

Another way to estimate mortality indirectly is to model population decay using population size estimates over time (using an exponential relationship and the Monte Carlo method). Cooper et al. (2012) used this method to estimate green crab survival rates using population data reported in Cohen, Carlton, and Fountain (1995). They created a histogram of survival rates, which peaked at the 0.15 - 0.25 ranges.

2.6 Sex Ratio

The sex ratio of green crabs has been reported to be dominated by males in many studies (e.g. Sharp et al. 2003; Baeta et al. 2005; Lyons et al. 2012). However, these data may be a result of trapping bias as females are less active in the summer when they are ovigerous and molting, and will often move to deeper water (Ropes 1968).

2.7 Habitat Use

Habitat and environmental factors are important components to consider in any discussion about demography or population dynamics, as they are important determinants

on how a population responds to any pressures (including control strategies) (Cosham, Beazley, and McCarthy 2016). Understanding habitat use can help with predicting range expansion, potential impacts on the invaded ecosystem, outcomes for antagonistic interactions, and help predict likely locations for different life stages.

Green crabs have wide abiotic tolerances. They can be found at a depth of 6 m all the way to the shoreline, with larger adults typically found at deeper waters (Crothers 1968). The salinity tolerance for green crab is 4 to 54‰, and they can tolerate temperatures from 0 to 33°C (Breen and Metaxas 2009). Green crabs have even been shown to survive periods of extreme drought (Bessa et al. 2010) and are capable of surviving for three days out of water (Darbyson et al. 2009). These wide tolerances and high resilience contribute to the green crab's invasion success and continued range expansion.

Green crabs utilize a variety of habitat types in the intertidal and subtidal. They are most often found under rocks or shells, buried in sand or mud, in salt marshes, in eelgrass beds, or in mussel or oyster beds (Crothers 1968; Klein Breteler 1976; Thiel and Dernedde 1994; McDonald, Jensen, and Armstrong 2001; Jensen, McDonald, and Armstrong 2002). These habitats provide refuge for green crabs from predation, desiccation, temperature changes, and shields them against strong currents or wave impacts (Jensen, McDonald, and Armstrong 2002). Unfortunately, they are also capable of competitively displacing native crustaceans from these refuge habitats (McDonald, Jensen, and Armstrong 2001), and altering the habitats in the ecosystem that they invade. For instance, they can uproot eelgrass beds (Davis, Short, and Burdick 1998; Malyshev and Quijón 2011; Garbary et al. 2014), and eat bivalves that create biogenic structure in

the ecosystem (Grosholz et al. 2000; Rossong et al. 2012). Since it is well established that higher habitat complexity decreases predation rates (Diehl 1992; Ebersole and Kennedy 1995; Finke and Denno 2002; Hill and Weissburg 2013), green crab habitat alteration is placing those native species at greater predation risk with reduced access to food.

2.8 Knowledge Gaps and Future Directions

Reviewing the literature on population dynamics of green crabs allowed for the identification of knowledge gaps and potential future directions for research on fecundity, larval stages, longevity, and natural mortality rates.

One area for future research is investigating the abiotic factors that determine whether green crabs have one or two broods per year. This seems to depend on temperature and length of the summer (warmer) season. However, little information is available about which locations have more than one brood, what percentage of crabs have more than one brood, or what temperature (or length of the warmer season) is required to trigger and allow a second brood. This is an especially important point for future research as climate continues to change and ocean temperatures warm up, which has been shown to affect fecundity in many marine organisms (e.g. Tanasichuk and Ware 1987, Pörtner et al. 2001, Hirst and Bunker 2003).

All studies examining larval stages have been conducted in a laboratory setting, and the results are quite variable (see Table 2.2). There are many difficulties associated with raising larvae in a laboratory setting such as controlling turbidity (Dawirs 1985). Further work should include perfecting the techniques and conditions required to successfully raise larvae in a lab setting. Additionally, continued work on examining

larval survival and abiotic tolerances will help to clarify whether the large variations in the current data are due to small sample sizes, and inconsistent laboratory conditions, or whether it accurately reflects the large variations in natural larval survival.

Age is a very difficult parameter to estimate for crustaceans because they molt regularly and do not keep any hard body parts that are often used to age other organisms. Although there are several estimates on longevity in the literature (Table 2.5), it is not always apparent how these studies derived these estimates. A clearer method for how to estimate longevity in green crabs is needed for consistency across geographic regions, such as the method developed by Kilada et al. (2015).

Natural adult mortality has been identified as one of the most important, but least understood parameters for fishery models (Hewitt 2008). The linear regression model based on longevity (Hoenig 1983) has been identified as the best method for estimating natural mortality in crabs, but again, this highlights the need to have a consistent method for estimating longevity.

Finally, this summary of green crab demography information can be used to help facilitate the creation of population models for green crabs. Models can help predict the green crab population response to different removal strategies. Modeling is especially useful when resources are limited, and determining the most effective removal strategy is always valuable. Currently, many removal strategies are initiated to control green crab populations without knowing whether removal efforts will have any impact on the population (e.g. Duncombe 2014). Several management and mitigation strategies for green crabs have already been considered including use of parasites (Lafferty and Kuris

1996; Thresher et al. 2000), chemicals (Hanks and Roberts 1961), and selective harvest of adults (Walton 2000; Duncombe 2014).

The creation of a green crab fishery is also being explored in some areas of Atlantic Canada with the aim of controlling green crab populations while providing an alternative fishery resource for inshore fishermen (St-Hilaire et al. 2016; Poirier et al. 2016). Only one published green crab population model has been created to date (Kanary et al. 2014), and I suggest that the creation of additional models would help to validate the predictions made by the current models, and could go further to include more variables to increase the model's ability to accurately reflect reality. I hope that by gathering the available green crab demography information together in this review, it will help assist in the creation of future population models for green crabs (see Chapter 6).

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CHAPTER 3

Hide and seek: Habitat-mediated interactions between European green crabs and native mud crabs in Atlantic Canada (*)

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I declare that the co-authors identified above collaborated with me in the provision and/or analyses of some of the data used in this chapter. However, I remain the first and main author of the publication and this thesis chapter.

3.1 Abstract

The non-indigenous European green crab (*Carcinus maenas*) has well documented impacts on many native species. In the Atlantic Canada region, the green crab distribution is increasingly overlapping with the distribution of mud crabs (primarily *Dyspanopeus sayi*), a prominent native species. Despite the potential for antagonistic interactions, the relationship between the two species has not been examined, particularly in the context of the diversity of habitats available in the region. This study used observational beach-seine data collected between 2009 and 2013 from the southern Gulf of St. Lawrence to explore the temporal and spatial relationships between mud crabs and green crabs, and detected a negative relationship between these species. 24h laboratory experiments examined their predator-prey interactions, and assessed the influence of habitat complexity on the outcomes of these interactions. Mud crabs and similar-sized green crabs collected during July and August of 2010 and 2011 were used as prey for large green crab. These predators consumed almost twice as many mud crab compared to juvenile green crab in the two less structured habitats (no substrate or sandy substrate),

but predation rates were statistically similar in oyster bed habitat. In that particular habitat, mud crab mortality dropped by ~65% whereas the generally lower mortality affecting juvenile green crabs was unaffected by habitat. These results suggest that complex habitats mediate predator-prey interactions, and dampen the effect of green crab prey preference. As green crab continues to invade areas dominated by mud crabs, they may threaten the sustainability of this native species.

3.2 Introduction

Predation plays a major role in the regulation and structuring of prey populations and communities (Connell 1961; Luppi et al. 2001). On sedimentary bottoms, most predators and prey are mobile and have developed behavioral abilities to seek prey and avoid predators, respectively. Decapod crustaceans, in particular crabs, are an interesting group of predators given their broad range of interactions and the consequences of these interactions for other species. For example, some predatory crabs have been shown to affect size structure of bivalve prey (Peterson 1982) whereas others structure communities (Botto and Iribarne 1999) or modify the distribution or behavior of individual prey, including decapod species (McDonald et al. 2001). It is well established that the habitat in which predators and prey interact has a strong influence on the outcome of these interactions (Diehl 1992; Ebersole and Kennedy 1995; Finke and Denno 2002; Hill and Weissburg 2013). In complex habitats (seagrass, seaweed, or bivalve beds, for example), prey may seek refuge from predators more easily than in structurally simple habitats such as muddy or sandy sediments. Meanwhile, predators may become less efficient at foraging for prey (Crowder and Cooper 1982).

The spread of marine non-indigenous predators provides an opportunity to study predator-prey interactions in relation to habitat (Sih et al. 2010). Native species may be naïve or unprepared to avoid or overcome mortality due to new predators, or these predators may disrupt well-established interactions that often allow native species to persist (Ricciardi and Atkinson 2004; Paolucci et al. 2013). In many examples, the introduction of a new predator has also displaced or caused local extinctions of native prey, in some cases leading to declines in overall biodiversity (Mills et al. 1993; Cohen et al. 1995; Grosholz and Ruiz 1996). In this context, it is important to gain insight into how different factors, including new predators and habitat complexity, interact to affect the outcome of predator-prey interactions.

The European green crab (*Carcinus maenas* Linnaeus, 1758) is an invasive species in various parts of the world including North America, South Africa, Australia, South America, and Asia. Green crabs first invaded the eastern American coast in 1817, and expanded northward to Maine by the early 1900s (Audet et al. 2003). Over the next 50 years, green crabs continued their northward colonization up to the Bay of Fundy in Canada, reaching Prince Edward Island by 1997 (Audet et al. 2003). The green crab is a voracious predator that feeds on an array of small bivalves and small crustaceans, including younger life stages of its own species (Baeta et al. 2006). Previous research indicates that native prey survival when facing a predator like the green crab will be higher in habitats that are structurally more complex (Crowder and Cooper 1982; Fernandez et al. 1993; Fernández 1999; Hill and Weissburg 2013; Hernández Cordero and Seitz 2014). However, it does not elucidate how habitat will affect green crab interspecific and intraspecific prey preference and predation rates.

Several studies have shown that green crabs prey upon or displace native crustaceans from their habitat (McDonald et al. 2001; Jensen et al. 2002; Rossong et al. 2006; Williams et al. 2009). This may become the case for mud crabs (*Dyspanopeus sayi* Smith, 1869), a small species native to Canada that is well established in habitats like sandy and muddy sediments and oyster beds. Because mud crabs and green crabs use some of the same habitats, it has been suggested that these species may interact negatively as green crab populations continue to grow and spread (Breen and Metaxas 2009). My own observations (unpublished) and observations of others (Lloyd 1968; Cushing 1991) also suggest that adult green crabs are predators of mud crabs and juvenile green crabs, which raises two related questions: is there evidence of a spatial/temporal negative relationship between these species? And if so, are predator-prey interactions a mechanism mediating this relationship?

In this study I assessed abundance data from a large dataset of beach seine surveys conducted in multiple estuaries in the southern Gulf of St Lawrence over the course of five years, to explore potential negative relationships between green crabs and mud crabs. Oyster beds and sandy sediments are common habitats throughout this region. I then conducted experiments that manipulate habitat complexity to investigate how habitat influences adult green crab predation rates and prey preferences when presented with small native mud crabs and juvenile green crabs. In addition to mortality, my study also assessed injury rates in order to examine the incidence of sub-lethal effects. My null hypothesis was that prey mortality and injury levels would be similar between prey species (mud crab and green crab) regardless of habitat type (no substrate, sandy sediments, and oyster bed mimics). However, based on previous studies that examined

the effects of habitat complexity on predator-prey relationships, I expected prey mortality to decrease with increasing habitat complexity (Crowder and Cooper 1982; Fernández et al. 1993; Fernández 1999; Hill and Weissburg 2013; Hernández Cordero and Seitz 2014).

3.3 Methods

3.3.1 2009-2013 Crab monitoring in the Southern Gulf of St Lawrence

The relative abundance of crab species (including green crab and mud crab) was estimated in 29 estuaries of the southern Gulf of St. Lawrence using beach seine nets as part of the Community Aquatic Monitoring Program (CAMP) (Fig.3.1). The CAMP program is a Citizen Science monitoring program that collects data about fish, macro-crustaceans (including crabs) and local physical parameters in estuaries of the Canadian Maritimes: New Brunswick (NB), Nova Scotia (NS) and Prince Edward Island (PEI). A detailed description of the study area and sampling methodology can be found in (Weldon et al. 2005); briefly, six stations per estuary were sampled once per month during June, July, and August of each year by pulling a 30 X 2 m (6mm mesh) beach seine in the shallow subtidal of each station. Sandy sediments and scattered oyster beds, two of the habitats represented in the laboratory experiments (see below) in addition to eelgrass beds and salt marshes, are prominent features on a large majority of these estuaries.

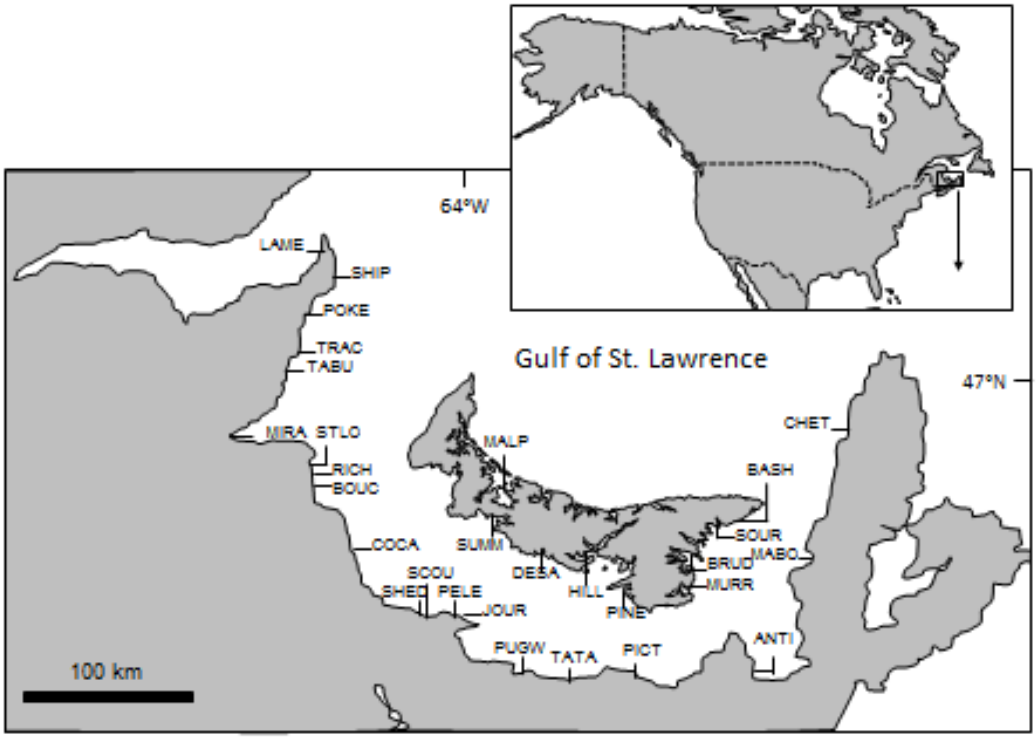

Figure 3.1: Outline of the study area and map of the 29 sample locations. Estuary codes are as follows: ANTI: Antigonish; BASH: Basin Head, BOUC: Bouctouche; BRUD: Brudenell; CHET: Cheticamp; COCA: Cocagne; DESA: Desable; HILL: Hillsborough; JOUR: Jourimain; LAME: Lameque; MABO: Mabou; MALP: Malpeque Bay; MIRA: Miramichi; MURR: Murray River; PELE: Cap Pelé; PICT: Pictou; PINE: Pinette; POKE: Pokemouche; PUGW: Pugwash; RICH: Richibouctou; SCOU: Scoudouc; SHED: Shediac; SHIP: Shippagan; SOUR: Souris; STLO: St. Louis de Kent; SUMM: Summerside; TABU: Tabusintac; TATA: Tatamagouche; TRAC: Tracadie.

For each estuary, the number of crabs per month (regardless of size) was integrated into relative abundances of each species per summer season (year). Hence, relative abundances per species correspond to percentages over the total number of crabs (not the mean number of crabs) collected during that season. In the estuaries included in CAMP, mud crabs refer to members of the family Panopeidae. However, a large majority of these mud crabs (>95%) belong to *Dyspanopeus sayi* whereas the white-finger mud crab *Rhithropanopeus harrisii* (Gould, 1841) was a considerably less common second

species. In estuaries of southern PEI, where large number of samples of mud crabs were collected over three consecutive summers (2009-2011), *D. sayi* represented ~97% of all the mud crabs collected (Pickering 2011).

3.3.2 Crab collection and tank set up for experimental work

During July and August of 2011, large adult green crabs (70-80 mm carapace width) were periodically collected from the Souris River estuary on the eastern shore of PEI (Fig.3.1). In order to avoid biases associated with gender or the molting process, only intact (uninjured) males without signs of molting were retained and subsequently used as predators. Simultaneously, juvenile green crabs and adult *D. sayi* mud crabs (both 25-30 mm carapace width) were regularly collected from North River (Hillsborough estuarine system, southern PEI; Fig. 3.1). Only intact individuals of both species were retained and used as prey in the experiments described below. Habitats in which both species were collected included extensive sedimentary bottoms (particularly sandy sediments) associated with oyster, mussel and eelgrass beds. These sites were also considerably similar in terms of water quality and tide regimes. Predators and prey were not "naïve" to each other or to the habitats used in the experiments. Experiments were run in glass tanks with dimensions 21.6 cm x 41 cm x 25 cm high, filled with prepared seawater made from chlorinated well water from the University of Prince Edward Island and Instant Ocean (25 ppt, 18-20°C). Each tank had an air stone and its top and sides were covered to minimize external visual stimuli and prevent crab escape (Palacios and Ferraro 2003). Three distinct habitat mimics representing increasing habitat complexity were prepared in these tanks: no substrate (water only), sandy sediment habitat (tanks were fitted with a 3

cm layer of cleaned sandy sediments), and oyster bed habitat (tanks were fitted with a 3 cm layer of clean oyster shells). Although tanks with water were admittedly an artificial habitat, they provided the conditions in which prey could not physically hide from predators. As for the two more complex habitats, sandy sediments were originally collected from Brackley Bay, PEI (fine to medium sands, ~0.5-1.0 mm grain size) whereas oyster shells (*Crassostrea virginica*) were collected from North River (~2-4 cm SL). Before all experiments, both sandy sediments and oyster shells were repeatedly washed and filtered in order to remove any live organisms that could act as alternative prey. Water and substrate mimics were replaced after each individual experiment.

3.3.3 Experimental procedure

Two separate experimental designs aimed to assess predator feeding rates and preference for prey, both in relation to habitat. The first design assessed the effects of a predator (large green crab) on five small prey (either mud crabs or juvenile green crabs). The second design examined predator preference upon both prey species combined: three mud crabs and three juvenile green crabs in the same tank. For each design, 15 replicates per treatment were conducted. Individual predators were starved for 48 hours prior to the experiment in order to standardize hunger levels (e.g. Mascaró and Seed 2001). In addition, new predators were used for each experiment to avoid the risk of biased results due to learning (Cunningham and Hughes 1984). Two response variables were measured: prey mortality rate (i.e. the number of individuals of each prey species that were found dead after 24 h) and prey injury rate (the number of individuals with missing claws or legs or signs of damaged carapace after 24 h). All the experiments were initiated in the

morning (~10 AM), and although they lasted 24 h, systematic observations were made after 0.5, 1, 2, 3, 4, 5, and 24 h in order to identify potential trends in timing or period of most intense foraging (e.g., Pickering and Quijón 2011). The sides and top of each tank were covered to control for light exposure. As expected, most predation occurred during the night hours and given the lack of any consistent trends during the first 5 h, results are reported (and statistically analyzed) for the 24 h period only.

3.3.4 Statistical Analyses

2009-2013 Crab monitoring in the Southern Gulf of St Lawrence

I explored the relationships among all crab species collected each year and from each of the 29 estuaries that had consistent records between 2009 and 2013. Data were analyzed using the multivariate method "Principal Coordinate Analysis" (PCoA) available in PRIMER v.6. routines (see Clarke and Gorley 2006 and Anderson et al., 2008). The PCoA was used as a linear ordination of species annual relative abundances in the 29 estuaries of the southern Gulf of St. Lawrence. The PCoA creates a matrix of distances between points using the well-known Bray-Curtis similarity index based on square-root transformed data. PCoA processes data like a Principal Component Analysis (PCA) which entails linear combinations of the variance of multivariate data. However, unlike PCA the PCoA has the advantage of being able to use any distance measure (including Bray Curtis) and not just Euclidean distance to identify correlations (see Anderson et al., 2008). These correlations among crab species and axes strengths are reported as Pearson's correlations (r). The program also displays vectors that correspond to the increasing relative abundance of the crab species under analysis. The outcome of the

analysis provides a visual picture of the relative similarity (spatial clustering) of data points and captures relevant between-year variation.

Mean annual abundance estimates of mud crab and green crab were modeled over time using simple linear regression in Minitab 17 (2010) with the goal of identifying potential changes over time for the entire study area. In the analysis the mud crabs (Panopeidae Ortmann, 1893) species were pooled due to difficulties distinguishing them apart. Crab relative abundances were square root transformed to better meet the assumptions of linear models. For this analysis, only 21 (of the original 29) estuaries were considered, given that in 8 of these estuaries there were no records of green crab invasion/establishment during the study period (i.e. for the regression analysis, n=125). Regardless, the outcome of a parallel analysis including all 29 estuaries was virtually identical.

Laboratory experiments

For the first design (predator feeding rates on individual prey species) I used the following two-way ANOVA model to examine mortality and injury rates as response variables separately:

Response variable = Prey + Habitat + Prey*Habitat + Error,

where *Prey* (mud crab or green crab) and *Habitat* (water, sediment or oyster bed) were considered fixed factors. When the interaction term was significant, pairwise comparisons using Tukey's honest significant differences were subsequently applied to

elucidate the influence of each main factor separately. The test corrected p-values for multiple comparisons.

For the second design (predator feeding rates on both prey species combined; hereafter referred as "preference"), I adapted a two-way ANOVA model again using mortality and injury rates as response variables:

Response variable = Prey + Habitat + Prey*Habitat + Tank (Habitat) + Error,

where *Prey* and *Habitat* were considered fixed factors, and *Tank* (*Habitat*) was considered a random factor. In this model, tank was nested within habitat (given that not every habitat is in every tank) as was considered the unit of replication in order to avoid potential pseudoreplication. When the interaction term was significant (i.e., effect of prey type on mortality differed by habitat type) pair-wise comparisons using Tukey's honest significant differences were applied to elucidate the influence of each main factor. Statistically significant differences for all linear models, including field and experimental analysis, were defined as $P \leq 0.05$.

3.4 Results

3.4.1 2009-2013 Crab monitoring in the Southern Gulf of St Lawrence

At least four crab species were identified from the beach seine samples: the invasive green crab and the native mud crab (primarily *Dyspanopeus sayi*, and potentially a small fraction of the white finger mud crab *Rhithropanopeus harrisii*), rock crab (*Cancer irroratus* Say, 1817), and lady crab (*Ovalipes ocellatus* Herbst, 1799). In the

analysis of the relationships among crab species, the PCoA explained 99.8% of the variance (Fig. 3.2). The first axis of the PCoA explained 75.7% of the relative abundance in crab species and was primarily associated with the variation of green crab (r = 1.0), mud crab (r = - 0.8) and rock crab (r = - 0.7). All correlations in this analysis were statistically significant (P <0.05, n=145). The second axis explained 24.1% of the variance and was associated with rock crab (r = - 0.7) and mud crab (r = 0.6). The relative abundance of green crabs and mud crabs was negatively correlated (r = - 0.8). Likewise, green crab and rock crab were negatively correlated (r = - 0.7) and rock crabs and lady crabs were less strongly but positively correlated (r = 0.5) (Fig. 3.2). The main clustering of data points was observed across the first axis towards the right side, where green crabs were numerically dominant (Fig. 3.2). Towards the end of the green crab vector, a circle identifies an overlap of 60 data points, including all five annual samples collected from seven different estuaries: Antigonish, Basin Head, Cheticamp, Mabou, Murray River, Pictou and Souris. Fig. 3.2 also illustrates between-year variation in several estuaries. For instance, Bouctouche samples were dominated by mud crabs early during the sampling period (2009-11) but are subsequently displaced towards the right side as green crabs enter the system and begin to dominate in abundance (Fig. 3.2). In contrast, samples from Malpeque Bay, an area not yet invaded by green crabs remained associated to high densities of mud crabs, towards the left side of axis 1 (Fig. 3.2).

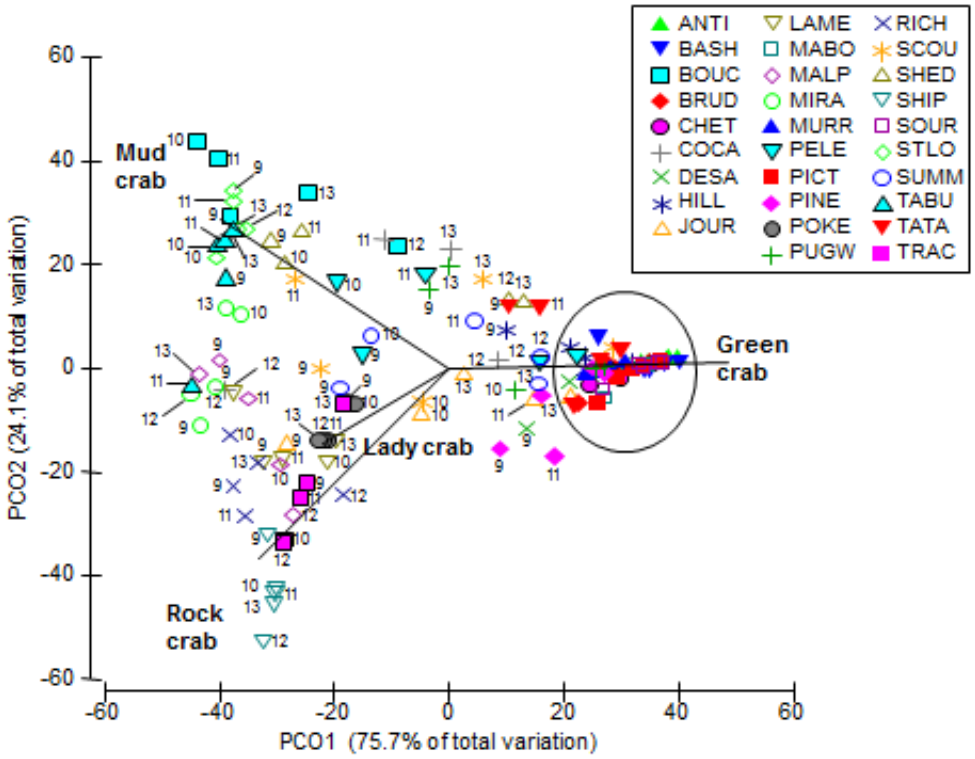

Figure 3.2. Results of the Principal Coordinates Analysis (PCoA) of four crab species in 29 estuaries of the southern Gulf of St. Lawrence from 2009-2013 (shortened to two digits). Years were removed from the encircled area due to the overlap of 60 data points, including all the points from ANTI, BASH, CHET, MABO, MURR, PICT, and SOUR, and most (4 out of 5) data points from BRUD, DESA and HILL. Estuary codes are similar to those shown in Fig. 3.1.

The annual green crab abundance per estuary ranged from 0 to 1084 individuals (the highest abundance for the study period was recorded in Basin Head in 2013). For mud crabs, annual abundances ranged from 0 to 1084 crabs, with the highest estimate recorded in Bouctouche in the 2010 season. Temporal trends for green crabs and mud crabs from a subset of 21 estuaries in which both species occur (Fig. 3.3) showed a significant increase in the number of green crabs over time ($r^2 = 0.8$, $F_{1,3} = 13.8$, $P = 0.034$). Relative number of green crabs for the entire study area increased from 59% to 82%. Conversely, mud crabs did not significantly decrease over the same period ($r^2 = 0.4$,

$F_{1,3} = 1.7$, $P = 0.279$), although a slight negative trend was apparent (Fig. 3.3). Temporal trends using data from the full set of 29 estuaries (not shown) were virtually identical.

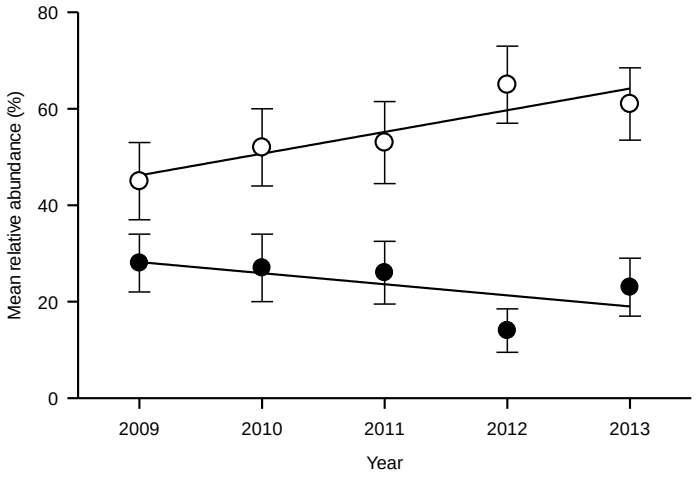

Figure 3.3. Mean (+/- S.E.) relative abundance of green crabs and mud crabs (open and filled symbols, respectively) in 21 estuaries of the southern Gulf of St. Lawrence over five years (n=105 for each point).

3.4.2 Green crab feeding rates and prey preference

For both mortality and injury rates, the results of the two-way ANOVA model indicated that habitat type, prey species, and their interactions were all significant ($P < 0.05$, Fig. 3.4, Table 3.1). Post-hoc Tukey honest significant difference tests showed that levels of mortality and injury for mud crabs were almost twice those for green crabs, except in oyster shell habitat, where they were not significantly different (Fig. 3.4, Table 3.1). Mortality and injury rates were similar across habitat types for juvenile green crabs. With regards to experiments assessing preference (Fig. 3.5), the results of the two-way ANOVA model indicated that for both mortality and injury rates, habitat type and prey species were significant, and that their interaction was significant for mortality (Table 3.1). Post-hoc Tukey honest significant difference tests showed that in general, mortality

and injury values for mud crabs were twice those for green crabs (Fig. 3.5, Table 3.1). Mortality and injury values were similar across habitat types for juvenile green crabs.

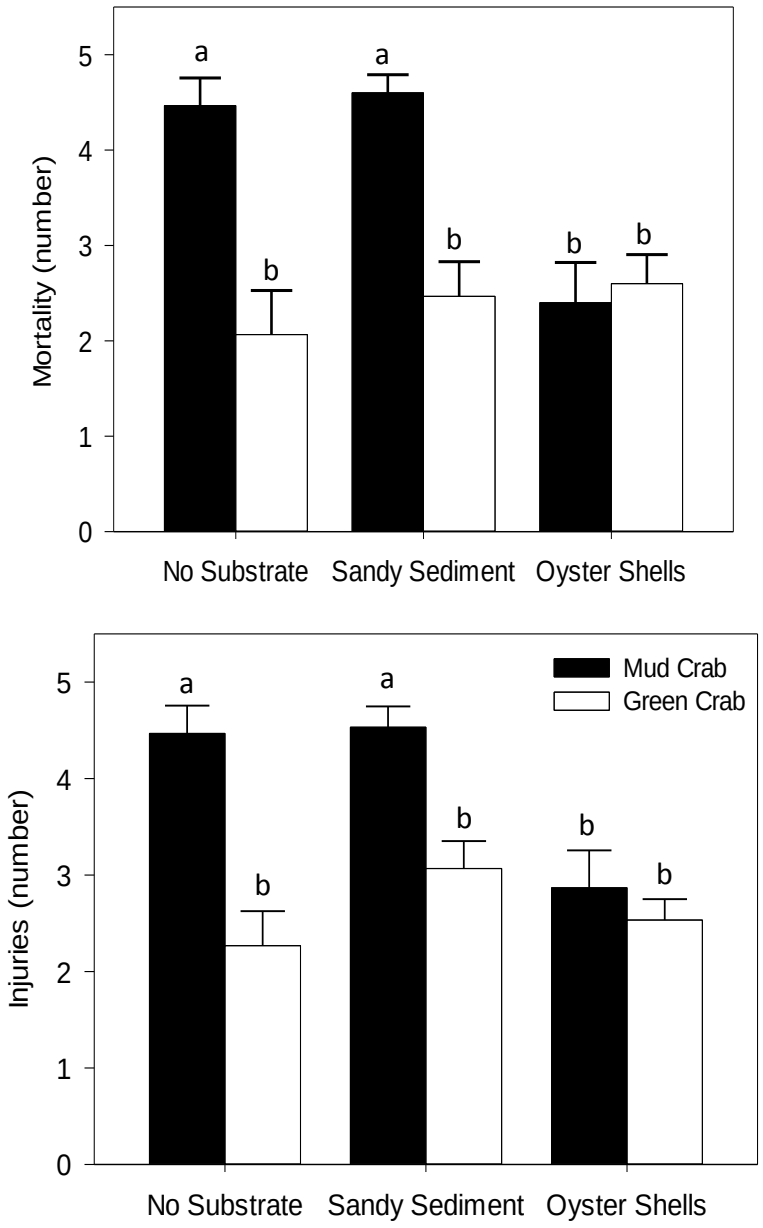

Figure 3.4: Mortality and injury data for individual prey species (five mud crabs or five green crabs) in three habitat types. Bars with different letter indicate a statistically significantly difference ($P < 0.05$). Error bars represent standard error.

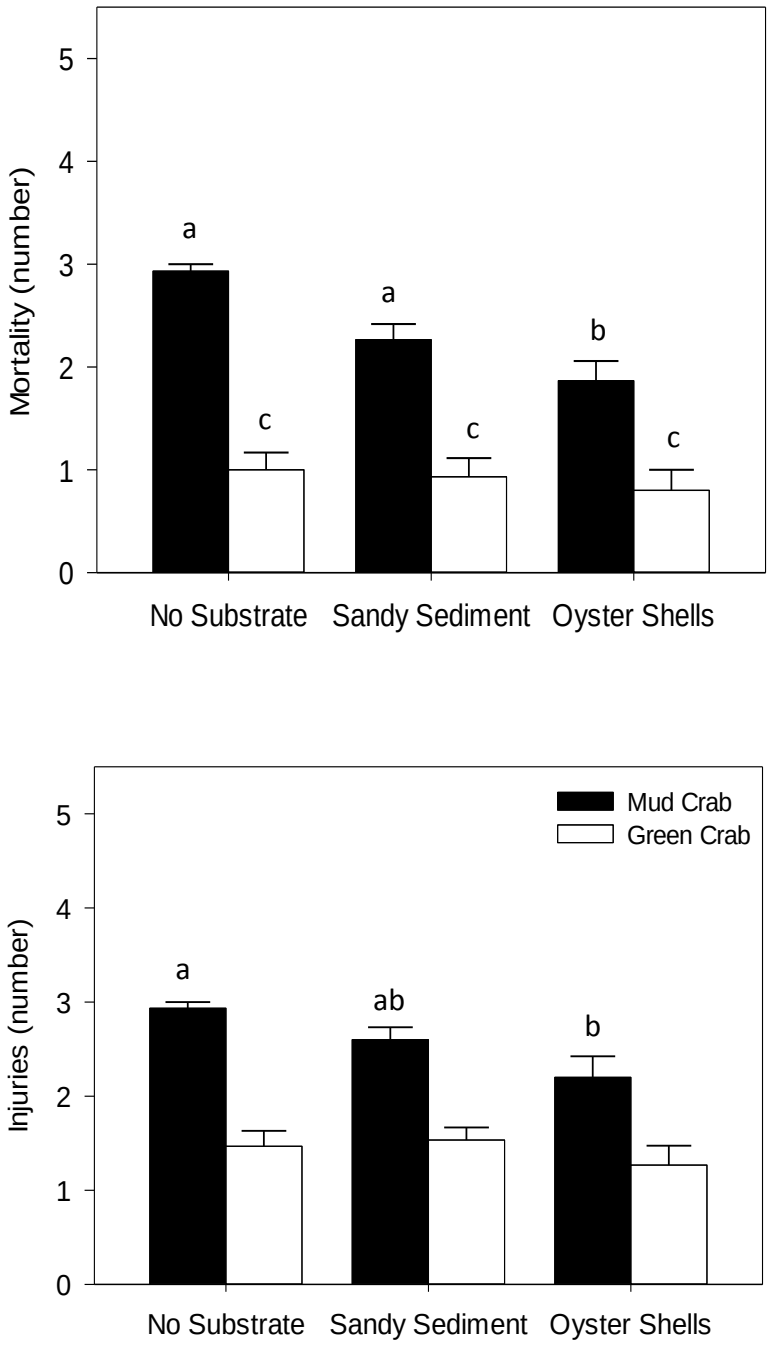

Figure 3.5. Mean (+/- S.E.) mortality and injury rates for trial run with combined prey species (three mud crabs and three green crabs) in three different habitat types (n=15). Bars with different letters indicate a statistically significant difference ($P < 0.05$). For injury rates, the interaction term was non-significant, so letters refer to significant differences among habitats (prey species was significant on each habitat).

3.5 Discussion

3.5.1 Patterns in estuaries of the Canadian Maritimes

Green crab populations continue to spread and grow in some areas of the Canadian Atlantic region (e.g. PEI and Newfoundland; Audet et al. 2003; Blakeslee et al. 2010). It is in these areas where green crab populations have been hypothesized to be most aggressive (Rossong et al. 2012) and therefore most likely to negatively interact with native species. The large CAMP dataset spanning 5 years and 29 estuaries provides comprehensive evidence of a negative relationship between this invasive species and at least two native crab species, including the mud crabs (primarily *D. sayi*), the focus of this study. Such negative relationship, of course, may not be causally related to green crab aggressiveness or their predation on mud crabs. In fact, for a spatial scale like the one studied here, a negative relationship is most likely linked to multiple factors, related or not to predation. Negative relationships between green crabs and rock crabs have already been partially addressed in a few laboratory and field studies (Bélair and Miron 2009; Gregory and Quijón 2011; Matheson and Gagnon 2012). However, the strongest negative correlation detected here, between green crabs and mud crabs, has not previously been studied in detail. Several possible mechanisms could explain this negative relationship including but not restricted to physiological tolerance, habitat variation, competition for food or other resources, and predation.

Differences in physiological tolerance would easily segregate coastal populations and species (Hunt and Behrens Yamada 2003). However, such differences are unlikely to drive a negative relationship between these two species. Mud crab and green crab temperature, salinity, and depth tolerances are both quite broad and fairly similar to each

other (Breen and Metaxas 2009). In addition, CAMP sampling sites are purposely located within a range of salinities to ensure samples from each estuary come from brackish waters and not from freshwater and marine conditions (Weldon et al. 2005). Alternatively, spatial or temporal variations in productivity or the availability of good quality habitat may easily contribute to the variation in crab abundances. For instance, species like mud crabs and green crabs use habitats like oyster, mussel or eelgrass beds recurrently (Kneib et al. 1999), so their presence and distribution are likely critical for some stage of the crabs life cycle (e.g. Thiel and Dernedde 1994). As discussed below, oyster beds are highly structured in comparison to habitats like sandy flats, and should be preferred habitat not only for the purpose of predator refuge (Grabowski 2004). Highly structured habitats embedded within more uniform sandy sediments reduce risk of desiccation during low tide conditions and may enhance local food availability (Thiel and Dernedde 1994). Oyster beds and sandy sediments are widespread in the southern Gulf of St. Lawrence. Nonetheless, it is difficult to quantify their area or availability in the 29 estuaries included in this study due to the lack of consistent reports. Most likely, variations in these habitat characteristics (presence, area, distribution) would interact with slight changes in water characteristics and influence crab distribution and dynamics.

Negative mud crab – green crab interactions may be also associated with competition for food or habitats as those identified above. These interactions are common among crustaceans (e.g. Hunt and Behrens Yamada 2003) including green crabs (Rossong et al. 2006). In addition to the shallow subtidal, mud crabs thrive on mid-low intertidal oyster, mussel, and seaweed beds that are also a preferred substrate of juvenile green crabs (Day and Lawton 1988; Hedvall et al. 1998). It follows that potential

interactions between small crabs of both species can occur if such beds are small, patchy, or limited in number. The likely consequence of these interactions would be displacement or local exclusion of one of the species. The same applies to potential migrations of either type of small crab into deeper waters or upper intertidal areas (beyond seine net reach) as a response to competition. A fourth mechanism to explain the negative relationship between green crabs and mud crabs is the one further addressed in this study: predation. Predator-prey interactions were expected to operate in this system given the obvious differences in size between large and small crabs (potential predator and prey), the aggressive nature of adult green crabs (Rossong et al. 2006), and anecdotic evidence suggesting a green crab preference for mobile prey such as small crabs (P Quijón, unpublished). As addressed in detail below, it is also plausible that habitat and the occurrence of green crab cannibalism events (Moksnes 2004; Almeida et al. 2011) plays a role in these interactions and that was the reason to assess both factors in our experiments.

The results of PCoA and regression analyses do not necessarily imply that predation (or for that purpose competition or habitat variation) is the factor driving the dissimilar patterns of green crab and mud crab populations. These analyses provide further evidence of the growth and expansion of green crabs in the southern Gulf of St. Lawrence (Audet et al. 2003; Blakeslee et al. 2010): while the regression shows a significant increase in the relative abundance of green crabs, the PCoA provides local evidence of changes in crab composition as a result of the recent invasion of green crabs. The changes associated to this expansion are reflected in the negative relationship with mud crabs, particularly along the prominent mud crab – green crab axis of the PCoA.

However, I must be cautious with regards to the interpretation of these numeric changes: although I provided experimental evidence of one of the mechanisms by which green crab can affect mud crabs (see below), the temporal decline in mud crab relative abundance was not significant.

3.5.2 Predation as a mechanism to explain negative relationships between species

My results did not support the null hypothesis that prey mortality and injury rates would be similar between species and among habitats. Large green crabs consumed and injured significantly more mud crabs than juvenile green crabs when presented with a single type of prey and when given the choice between both species. Furthermore, I detected clear mortality and injury differences among habitat types for the native mud crab.

3.5.3 The influence of prey

Prior studies examining brachyuran crabs as prey have already identified some of the possible mechanisms behind preference and feeding rates. Kuroda et al. (2005) suggested that differences in predation rates upon two preys were related to their different burrowing abilities to escape predation. Similarly, Kneib et al. (1999) suggested that the less-preferred prey in their study was quicker and more difficult to capture than the alternative (preferred) prey. Alternative mechanisms include differences in prey palatability, caloric value, predator's search time, and prey defensive capabilities (Ellis et al. 2012). There is no published evidence comparing palatability and caloric values of mud crabs vs. juvenile green crabs, and it would be unwise to consider them similar

simply because they are of similar size. However, I do suggest that there are differences associated with predator search time and prey profitability in relation to habitat that could explain some of the preferences in my experiments (see below). Studies on the ability of prey to escape or defend themselves are uncommon in decapods, but Ellis et al. (2012) found that these two factors explained seagulls' preference for Jonah crab (*Cancer borealis* Stimpson, 1859) over green crab and rock crab.

Green crabs have been found to be less susceptible to predation than other species because of their cryptic coloration against dark backgrounds like mussel beds (Dumas 1993). Although there are no studies comparing green crabs with mud crabs, the fact that green crabs are skillful at hiding (using coloration or other mechanisms) may confer an advantage. Greater difficulty in detecting prey generally translates into higher energy costs for the searching and potentially handling of that prey. If mud crabs are less skillful at hiding than green crabs, optimal foraging theory (Pyke et al. 1977) and the concept of profitability (Norberg 1977) would explain the preferences observed.

Another intuitive explanation for my results relates to inclusive fitness (*sensu* Schausberger 2003). In general, predators are expected to prey upon heterospecific prey rather than upon conspecifics (cannibalism). Inclusive fitness reduces the likelihood of killing related individuals (Schausberger 2003) and this should be advantageous for species undergoing population growth, as invasive species are. In my experiments, juvenile green crab mortality and injury rates were low in the "no sediment" trials where they had no possibility to hide or disguise themselves, which suggests that avoidance of cannibalism may be occurring. Cannibalism has been recorded in green crabs at low rates (Baeta et al. 2005; Ropes 1968), which suggests that cannibalism avoidance may be

another possible mechanism to explain the preference and feeding rates observed in this study.

3.5.4 The influence of habitat

Mud crab mortality and injury rates decreased with increasing habitat complexity. This result is consistent with a well-developed body of evidence that suggests that increasing habitat complexity reduces prey mortality (e.g., Fernandez et al. 1993; Dittel et al. 1996; Fernández 1999; Langellotto and Denno 2006; Stoner et al. 2010; Hill and Weissburg 2013; Hernández et al. 2014). The most common mechanism to explain the influence of habitat complexity is a decrease in the rate of predator-prey encounters. In complex habitats, prey may seek refuge from predators more easily, or predators may be less mobile or efficient at finding and catching prey compared to less structured habitats (Crowder and Cooper 1982; Grabowski 2004).

Surprisingly, the pattern was quite different for the other prey species; juvenile green crab mortality and injury rates were unaffected by habitat complexity. I hypothesize two opposing mechanisms that could explain this result. First, juvenile green crabs are vulnerable to predation like any other small decapod seeking refuge in complex coastal habitats (Ellis et al. 2012). However, unlike most native species, juvenile green crabs may be as good at escaping predation in less structured habitats as they are in complex habitat. A second mechanism to explain why juvenile green crab mortality levels were unaffected by habitat is the exact opposite; juvenile green crabs may lack the ability to effectively use complex habitat to escape predation. Long et al. (2015) suggested that responding to predator presence by engaging in cryptic behavior (i.e.,

hiding in complex habitat) may be a learned behavior, and in some crab species, refuge-seeking behavior is known to develop with size and age (Johnson et al. 2008; Stoner et al. 2010; Pirtle et al. 2012). Under this hypothesis, I might expect that 'naïve' juvenile mortality would indeed be similar across habitat types, while the mud crabs (already adults in my experiment) would be expected to be more experienced and have a greater affinity for hiding in complex environments. Although both mechanisms are plausible and consistent with the mortality and injury rates reported in my study, I do not have direct evidence for either, so I call for further experiments to elucidate these mechanisms.

A major implication of this study is the potential detrimental effects of the loss of complex habitats, which according to my results, would have worse effects on native mud crabs than on juvenile green crabs. Two factors that have had adverse effects on numerous habitats in the east coast of North America, as well as other regions, are habitat destruction and invasion by the green crab. Green crabs predate upon bivalves (Palacios and Ferraro 2003; Miron et al. 2005; Pickering and Quijón 2011), including habitat-building species like oysters and mussels, leading to decreases in habitat complexity. Green crabs also uproot and graze on eelgrass (Malyshev and Quijón 2011), which has a detrimental effect on associated species and services (Heck et al. 2003). As green crabs continue to spread (Carlton and Cohen 2003), changes to native species, and in particular to habitats, will likely continue. This study documents a negative relationship between green crabs and mud crabs in the southern Gulf of St. Lawrence, and provides evidence that predation is one of the several mechanisms that may explain the association. My results suggest that if mud crabs are being displaced into habitat that is less structurally-complex, their survival rates at the local scale may further decrease.

3.6 Acknowledgements

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CHAPTER 4

Effects of habitat complexity on cannibalism rates in European green crabs (*Carcinus maenas* Linnaeus 1758) (*)

(*) Submitted as:

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I declare that the co-authors identified above collaborated with me in the provision and/or analyses of some of the data used in this chapter. However, I remain the first and main author of the publication and this thesis chapter.

4.1 Abstract

The habitat in which predator-prey interactions take place may have a profound influence on the outcome of those interactions. Cannibalism is an intriguing form of predation whereby the foraging by predators may contribute to the regulation of their own populations. This is particularly interesting in the case of invasive species, like the widely distributed European green crab (*Carcinus maenas*). This study explores how habitat complexity influences cannibalism rates in green crab populations of Prince Edward Island, Atlantic Canada. Both laboratory and field experiments were conducted to measure feeding rates by individual adult green crabs on standard numbers of prey. In the laboratory, experimental treatments mimicked unstructured to increasingly structured habitats: water, sandy bottom, oyster shells, mussel shells, oyster shells with sandy bottom, and mussel shells with sandy bottom. In those trials, adult green crabs consumed several times more juveniles on unstructured habitats than on the most structured ones, with a gradual decrease in predation rates across increasingly complex habitats. Field

inclusion experiments used the same approach and were conducted in sandy bottoms, sandy bottoms with a layer of oyster shells, and sandy bottoms with a layer of mussel shells. These trials showed similar patterns of decreasing feeding rates across increasingly complex habitats, but differences among treatments were not significant. These results support the idea that complex habitats have the potential to mediate predator-prey interactions, including adult-juvenile cannibalism in green crabs.

4.2 Introduction

Predation is an important determinant of the abundance and size of prey (Orth et al. 1984), particularly in sedimentary bottoms (see reviews by Peterson 1979; Wilson 1991, and Thrush 1999). It has also been demonstrated that the habitat in which predation takes place can influence its outcome (e.g. Diehl 1992; Ebersole & Kennedy 1995; Hill & Weissburg 2013): For instance, prey may seek refuge from predators more easily in complex habitats compared to structurally simple habitats, making predators less efficient at foraging for prey (Crowder & Cooper 1982). One intriguing form of predation is cannibalism, whereby under certain conditions predators may regulate their own populations (Lloyd 1968; Cushing 1991). Unfortunately, the influence of cannibalism in aquatic invertebrates is complex and not well understood (e.g. MacNeil et al. 1999; Dick 2005) and considerably less documented than the influence of interspecific predation (Claessen et al. 2003). This knowledge gap also applies to the shortage of studies addressing the influence of habitat on cannibalism rates.

Cannibalism in relation to habitat is particularly interesting in the case of invasive species. If I accept that this self-regulation mechanism has the potential to control

invaders' population growth (Govindarajulu et al. 2005), I should assume that it may also indirectly affect the invaders potential impact on native prey or biodiversity. The European green crab (*Carcinus maenas* Linnaeus 1758) is an interesting model species given its foraging abilities (Cunningham & Hughes 1984) and its use of a broad range of coastal habitats (Grosholz et al., 2000). In their invaded range, green crabs have been associated with declines of several commercially important bivalve species (Grosholz et al. 2000) and negative interactions with native crustaceans (Rossong et al. 2006; Breen & Metaxas 2008; Chapter 3). However, despite the common occurrence of cannibalism in green crabs, studies of green crab cannibalism in relation to habitat properties have lagged behind.

From the handful of available studies, stomach content analyses have estimated that cannibalism accounts for 2 to 4% (Chaves et al. 2010) or 6.7% (Baeta et al. 2005) of the diet of adult green crabs. Experimental studies have focused mostly on green crab cannibalism on newly settled crabs (e.g. Moksneset al. 1998; Moksnes 2004; Almeida et al. 2011) and suggest self-regulation during high seasonal settlement (Moksnes 2004). Other experiments have also shown that adult green crabs are able to cannibalize juveniles but prefer to prey on a native species of similar size (Chapter 3). Green crab cannibalism has also been observed, suggested or confirmed but not quantified by other studies (e.g. Ropes 1968; Elner 1981) without explicit consideration of habitat influence. Poirier et al. (2016) and my own preliminary observations suggest that cannibalism occurs often in a variety of habitats available in Atlantic Canada.

In this study, I manipulated habitat complexity to investigate its influence on adult green crab cannibalism rates on juveniles. My null hypothesis is that prey mortality rates

are similar regardless of habitat mimic. However, based on prior studies examining the effects of habitat complexity on various predator-prey interactions, I expect prey mortality to be the lowest in structurally complex habitats (e.g. Crowder & Cooper 1982; Fernandez et al. 1993; Fernández 1999; Hill and Weissburg 2013; Hernández Cordero & Seitz 2014; Chapter 3).

4.3 Methods

4.3.1 Crab collection

Large adults (predators, 70-80 mm carapace width, CW), and smaller green crabs (prey, 25-35 mm CW) were collected in North River, a shallow, soft-bottom estuary embedded in the larger Hillsborough estuarine system on the southern shore of Prince Edward Island (PEI), Canada (Fig 4.1). The physical characteristics of this and similar PEI estuaries have been summarized in Pickering & Quijón (2011) and Chapter 3. I used folding Fukui traps to target adult crabs (63 x 46 x 23 cm; 1.6 cm mesh; with wide, slit-like openings), and minnow traps to target smaller crabs (21 x 37 cm; 2.5 cm diameter openings; 0.5 cm mesh). All traps were baited with frozen mackerel (*Scomber scombrus*). To prevent unnecessary biases, only intact (uninjured) male green crabs were used (see Tummon Flynn et al. 2015), which were always starved for 48 hours prior to experiments to standardize hunger levels (Mascaró & Seed 2001). In addition, new individuals were used for each replicate to prevent biases associated to potential learning (e.g. Cunningham & Hughes 1984).

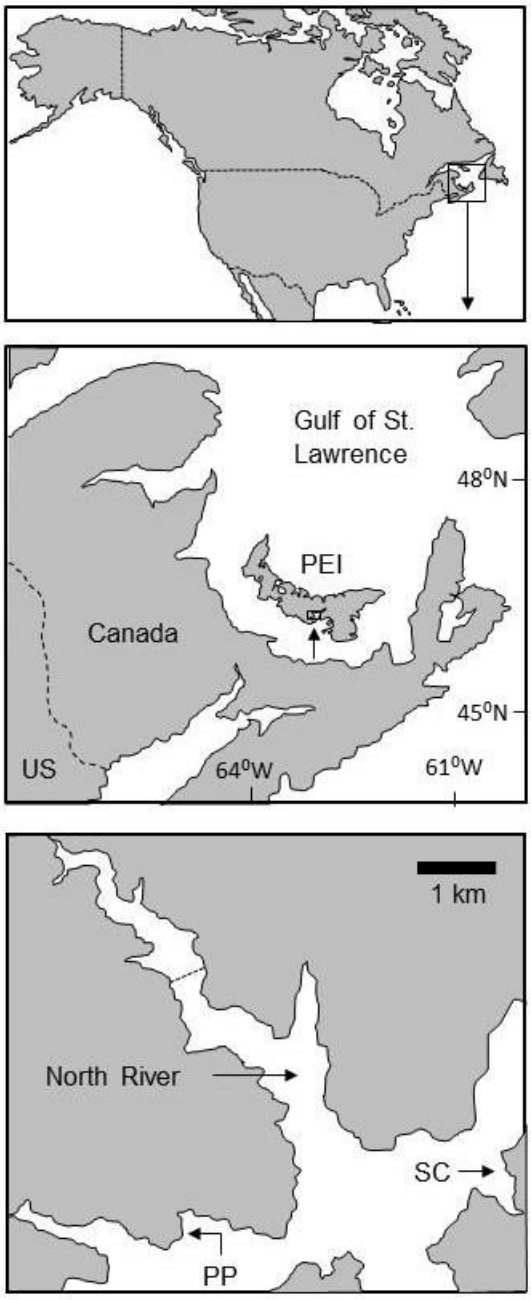

Figure 4.1 Outline of the study area, identifying the location of Prince Edward Island (PEI) within Atlantic Canada, and North River, Stewart Cove (SC) and Primrose Point (PP) all in southern PEI.

4.3.2 Laboratory experiments

Experiments were run in glass tanks with dimensions 21.6 cm x 41 cm x 25 cm, filled with prepared seawater (~25 ppt, 18 - 20°C). Each tank had an air stone, the sides

were covered and a lid placed on top to minimize external visual stimuli (Palacios & Ferraro 2003) and prevent crab escape. Six distinct habitat mimics representing increasing habitat complexity were prepared: no substrate (tanks with water only), sandy sediments (tanks fitted with a 3 cm layer of sandy sediments), mussel bed (tanks fitted with a 3 cm layer of mussel shells), oyster bed (tanks fitted with a 3 cm layer of oyster shells), mussel bed with sandy sediments, and oyster bed with sandy sediments. Sandy sediments (fine to medium sands, ~0.5-1.0 mm grain size) and oyster shells (*Crassostrea virginica*) were collected from North River (~5.0-6.8cm), and mussel shells (*Mytilus edulis*) from Primrose Point (~3.5 - 4.5 cm), all shorelines were located within the same estuarine system in which the field experiments were conducted (Fig. 4.1). Before their use in any experiment, sandy sediments, mussel and oyster shells were repeatedly washed and filtered in order to remove any live organisms that may act as an alternative prey. As with predators, water and habitat mimics were cleaned and replaced after each individual trial.

Once habitat mimics were prepared, five juvenile green crabs (prey) and one large green crab (predator) were added to each tank. My choice of number of prey was driven by a trade-off between having the highest possible number of prey available to measure mortality rates and field observations indicating that 5 is approximately the highest number of juveniles to aggregate in such a small area (P. Quijón, Pers. Obs.). Due to logistic and time constraints, replicates per habitat mimic were conducted on different years but approximately the same time during the summer season. Mussels with sand and oyster with sand trials were run in the summer of 2016, mussel shell trials were run in 2015, oyster shell, sand, and no substrate trials were run in 2011-13. In each individual

trial, prey mortality (i.e. the number of small crabs that died after a given number of hours) was recorded after 0.5, 1, 2, 3, 4, 5, and 24 hours in order to identify potential differences in timing of foraging and detect cases in which crabs die for unknown reasons or exhibited signs of molting (e.g. Pickering & Quijón 2011). Given that no consistent short-term trends were observed (most predation took place during the night hours) statistical analyses were only applied to the data recorded after 24 hours (i.e. at the end of the experiments).

4.3.3 Field experiments

Experiments were run in cylindrical wire cages (40 cm diameter, 26 cm height) arranged in parallel to the low intertidal area of Stewart Cove, PEI (Fig. 4.1; 46°13’06”N, 63°06’30”W). Each cage was embedded into a microtidal system characterized by sandy sediments and scattered mussel and oyster clumps, in addition to eelgrass beds (see Pickering & Quijón 2011 for a detailed habitat description). Three distinct habitat mimics representing increasing habitat complexity were prepared: bare sediment (sand), mussel bed (75% of the bottom of the cage was covered by mussel shells), and oyster bed (75% of the bottom of the cage was covered by oyster shells). As in the laboratory experiments, mussel and oyster shells were repeatedly washed and filtered before use in any experiment. The same number of prey was added to each cage (5 small green crabs exposed to one adult green crab). Prey mortality (i.e. the number of small crabs that died as a result of predation) was recorded after 36 hours.

4.3.4 Statistical Analysis

I analyzed the laboratory and field data separately. Data from a few replicates were not included in the analyses when experiments had either a predator or prey that showed signs of molting or died for unknown reasons. Data were analysed using the Kruskal-Wallis non-parametric model in Minitab 17 (2010), since the data violated the assumptions of the parametric one-way ANOVA. When significant differences among habitat mimics were found, I tested post-hoc pair-wise differences using Dunn's method. Statistical significant difference was defined as $P \leq 0.05$.

4.4 Results

4.4.1 Laboratory experiments

Crab mortality rates gradually decreased with an increase in habitat complexity (no habitat, sandy sediments, oyster shells, mussel shells, sand + oysters shells, and sand + mussel shells; Table 4.1). On average, mortality rates range between 0 and 3 crabs per day. A few significant differences among individual treatments were detected: mortality rates were significantly higher in the least complex habitats (first three treatments) than at the most complex ($H_{(5)} = 43.623$, $P < 0.001$, Table 4.1; Fig. 4.2).

Table 4.1. Laboratory habitat mimics, number of replicates (n) and juvenile green crab mean mortality (+/-S.E), in addition to median, mean rank, and Z values from Kruskal-Wallis comparisons. The H-value is presented at the bottom, and the results of post-hoc comparisons are illustrated in Figure 4.2.

Habitat Mimic	N	Mean mortality (S.E.)	Median mortality	Mean Rank	Z
No Sediment	13	2.80 (0.28)	3	54.5	3.43
Sandy Sediments	15	2.47 (0.13)	3	51.3	3.08
Oyster Shells	11	2.09 (0.27)	2	43.0	1.13
Mussel Shells	11	1.18 (0.36)	1	28.9	- 1.31
Sand + Oyster shells	11	0.63 (0.15)	1	20.7	- 2.72
Sand + Mussel shells	11	0.09 (0.09)	0	12.0	- 4.23
Overall	72			36.5	
H = 43.62; DF = 5; $P < 0.0001$					

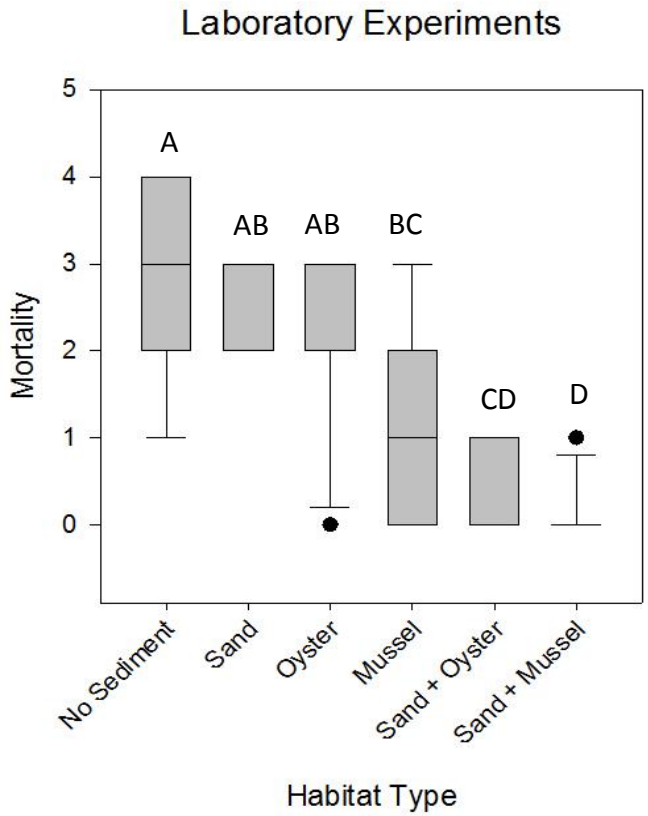

Figure 4.2. Box plots showing the results of the laboratory experiments: juvenile green crab mortality in six different habitat mimics. Boxplots show Q3, median, and Q1, bars show the range of the data, and dots represent individual data points that are 3/2 above and below the Q1 and Q3 respectively. Different letters at the top of the boxplots stand for significant differences among individual treatments. Mean values (+/- S.E.) for the same data are presented in Table 4.1.

4.4.2 Field experiments

A similar pattern was observed in the field experiments (cannibalism rates decreased with an increase in habitat complexity; Table 4.2). Prey mortality rates range between 1 and 2 crabs per day. Despite the differences, the Kruskal-Wallis non-parametric model indicated that mortality rates were not significantly different across habitat mimics ($H_{(2)} = 2.04$, $P = 0.360$, Fig. 4.3).

Table 4.2. Field habitat mimics, number of replicates (n) and juvenile green crab mean mortality (+/-S.E), in addition to median, mean rank, and Z values from Kruskal-Wallis comparisons. The H-value is presented at the bottom.

Habitat Mimic	**N**	**Mean mortality (S.E.)**	**Median mortality**	**Mean Rank**	**Z**
Bare Sediment	14	1.86 (0.26)	2	23.9	1.35
Oyster Shells	13	1.31 (0.37)	1	17.9	- 0.97
Mussel Shells	13	1.46 (0.35)	1	19.4	- 0.40
Overall	40			15	
H = 2.04; DF = 2; $P < 0.360$					

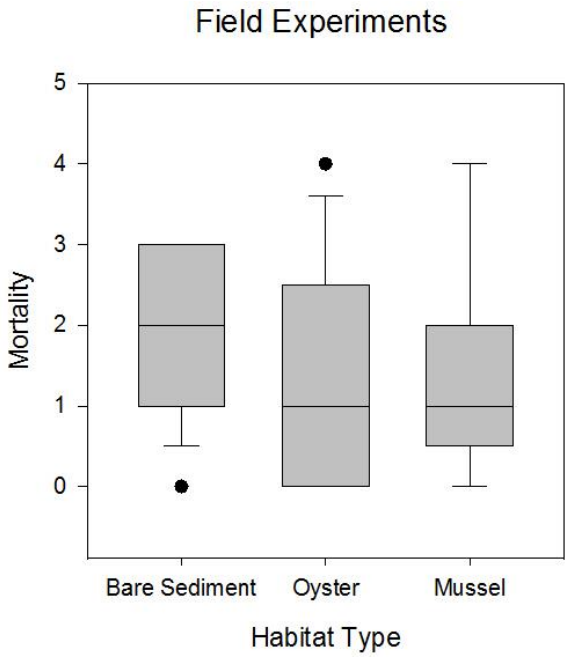

Figure 4.3. Box plots results from the field experiments, showing juvenile green crab mortality in three different habitat mimics. Boxplots show Q3, median, and Q1, bars show the range of the data, and dots represent individual data points that are 3/2 above and below the Q1 and Q3 respectively.

4.5 Discussion

My experiments provide quantitative evidence of green crab cannibalism and suggest that cannibalism rates may be affected by habitat complexity. Adult green crabs consumed between 1.8% and 56% of the prey items available in the laboratory experiments, and between 26% and 36% in the field experiments. Such mortality rates are considerably higher than those previously reported for green crabs through stomach content analyses (e.g. Baeta et al. 2005; Chaves et al. 2010) and other species of decapods (e.g. Amaral et al. 2009). With the exception of a prior study that focused primarily on interspecific interactions (Chapter 3), this is the first report on habitat complexity influencing adult-juvenile green crab cannibalism at this size range. To date, most other studies examining cannibalism in green crabs have focused on the predation

of juveniles by conspecific juveniles (e.g. Moksnes et al. 1998; Moksnes 2004; Almeida et al. 2011) or have collected evidence from stomach contents (Ropes 1968; Hughes & Elner 1979; Baeta et al. 2006).

The laboratory experiments showed that adult green crabs consumed more juvenile green crabs when habitats were structurally simple, compared to the habitats that were more structurally complex. These results are in agreement with a growing body of evidence that suggests that increasing habitat complexity decreases prey mortality (e.g. Fernandez et al. 1993; Dittel et al. 1996; Fernández 1999; Langellotto & Denno 2006; Stoneret al. 2010; Hill & Weissburg 2013; Hernández Cordero & Seitz 2014; Chapter 3). The most likely mechanism to explain the influence of habitat complexity is a decrease in the rate of predator-prey encounters. In complex habitats, small crabs seek refuge or hide from predators more easily. In addition, predators may become less mobile or less efficient at catching prey in these more structurally complex habitats compared to less structured habitats (Crowder & Cooper 1982; Grabowski 2004). Regardless of the specific mechanism in place, a reduction of predator's foraging efficiency in structurally-complex habitats would likely translate in lower predation and injury rates (e.g. Gehrels et al. 2016), as my results show.

I found a similar pattern but weaker differences between habitat mimics in the field experiments compared to the laboratory. This may be related to the less striking structural differences among the three habitat treatments (e.g. Hill & Weissburg 2013). Shells of oysters and mussels were expected to reflect increased habitat complexity in comparison to less structured sandy sediments (see Hernández Cordero and Seitz 2014). However, my mimics were set on sandy sediments which were an integral part of the

habitats as well and may have removed some of the distinctiveness among habitats. Visual observations suggest that juvenile green crabs did hide under oyster and mussel shells and therefore actively used this layer in an attempt to avoid predation, as they did in the laboratory. However, they also buried themselves within the sediment apparently gaining some degree of additional refuge. This limitation in my field design likely reduced among-treatment differences but I cannot ignore that cannibalism rates still showed a gradual decrease with increasing habitat complexity as they did in the laboratory. I am, however, cautious in my interpretation. Additional factors like the presence of alternative (infaunal) prey (e.g. Lutz et al. in press) or the increased size of the arenas (cages were ~40% bigger than tanks) may have reduced predator prey encounters (Crowder & Cooper 1982) and therefore contributed to diminish the differences among treatments.

My results, in particular the high rates of cannibalism detected, may direct further research about cannibalism in this and other decapods. In addition to prey mortality rates quantified here, predator and prey movements are part of the complex behavioral patterns that this type of species can display (e.g. Wong et al. 2005). This study may provide evidence about how visible mobile prey are to predators in the different habitat mimics, and about how predator search behaviour is indeed affected by habitat type. In addition, given that green crabs are not solely visual predators (e.g. Rittschof 1992; Robinson et al. 2011), visual stimuli are clearly not the only mechanism by which they forage or, in the case of small crabs, by which they potentially avoid predators. For instance, there have been cases in which prey burying themselves in the sand may have masked the odor plume on which predators rely for foraging (e.g. Kats & Dill 1998). Visual and chemical

cues are a likely venue for the study of intra-specific predator-prey direct and indirect interactions (Mirza & Chivers 2001; Mathis 2003) and a logical follow up for the experiments documented here.

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CHAPTER 5

A first approach to the assessment of a removal program on green crab population dynamics using a stage-based matrix model

5.1 Abstract

Matrix population models are helpful tools that can be used to aid the management of invasive species by predicting the consequences of mitigation strategies. Here, I used a simple, stage-based population matrix model to investigate population growth rate in green crabs (*Carcinus maenas*) and the theoretical effects of a harvesting program on this species. The stochastic model was parameterised using average life history values from the literature. Its outcome indicated that the green crab population would potentially increase in number by approximately 43% per year (λ=1.43) in the absence of harvesting or control measures. The model also suggested that removals of adults and juveniles have little effect on the population growth rate, indicating that harvesting alone is unlikely to result in a clear reduction of annual green crab abundance. These theoretical results coincide with the results of several green crab removal programs throughout its invaded range in North America.

5.2 Introduction

The management of many species is hampered by an inadequate understanding of their population dynamics (e.g. Crouse and Crowder 1987). Population matrix models, which are theoretical simulations used to model the size and age composition of populations as a dynamic system, may help to bridge this knowledge gap. Stage-base matrix models are flexible probabilistic tools that have been widely used to study the population dynamics of a species. They have been used to assess conservation efforts for endangered species (e.g. Kissel et al. 2014; Crouse and Crowder 1987; Crowder et al. 1994), and management strategies for invasive species (e.g. Govindarajulu, Altwegg, and Anholt 2005; Green et al. 2013; Dudas, Dower, and Anhold 2007; Barbour et al. 2011). In many cases, the predictions and suggestions derived from these models have resulted in changes to management and practices. For example, Rockwell et al. (1997) used a matrix model to suggest new strategies for controlling a population of snow geese. These suggestions were implemented by the U.S. Fish and Wildlife Service, and resulted in an increase in the harvest of snow geese in the following years (Caswell 2000; Rockwell and Ankney 1999). The management of invasive species often includes removal programs that aim to reduce or eradicate their populations (e.g. Miller 2001; Barbour et al. 2011). Removal strategies are often undertaken to control these populations without knowing whether removal efforts will have any impact on the population or what the direction that impact will be (e.g. Duncombe 2014; Therriault and Duncombe 2016; Matheson et al. 2016; Walton 2000). Population matrix models can be used to estimate the likely response of a population to various management scenarios, helping decision-makers to choose the most effective management option.

The European green crab (*Carcinus maenas* Linnaeus 1758) is an invasive species that has colonized various regions of the world including North and South America, South Africa, Australia, and Asia. Throughout this invaded range, the green crab is a dominant benthic predator, feeding on an array of small bivalves and small crustaceans (Baeta et al. 2006; Breen et al. 2008), competing for resources with other native species (Rossong et al. 2006; Matheson 2012), and altering critical habitat (Davis, Short, and Burdick 1998; Malyshev and Quijón 2011; Garbary et al. 2014). Management and mitigation strategies for green crabs have considered the use of parasites (Lafferty and Kuris 1996; Thresher et al. 2000), chemicals (Hanks and Roberts 1961), and selective harvest (Walton 2000; Duncombe 2014). While at least one removal program has had some success at reducing the green crab population in the Kejimkujik estuary (Mersey Tobeatic Research Institute and Parks Canada 2015), other removal strategies have resulted in little numerical decline in green crabs over time (Therriault and Duncombe 2016; Matheson et al. 2016; Walton 2000; Klassen and Locke 2007). Some of the studies that reported no decline did however show a decrease in size of crabs (carapace width) after sustained trapping (Walton 2000; Klassen and Locke 2007; Duncombe 2014). Those results suggest an effect on age composition or dynamics that, unfortunately, has not been thoroughly explored.

To date, most of the theoretical modelling done on green crabs has focused on range expansion and movement (e.g. Hines 2004; See & Feist 2010). These studies are useful for predicting when or where a species will potentially invade, but have not assessed how the population will respond to management strategies. Developing models about life history of crabs is challenging because there is little quantitative data available

with which to parameterise a model. In fact, long term population research on crabs has not been conducted or has not been frequently published. This may be in part due to the fact that mark recapture studies are difficult to conduct on animals that molt regularly and therefore do not retain hard body parts or distinguishing marks as they grow. The one study that has modelled the possible effects of control strategies on a green crab population, used an integrodifference equation model, and focussed explicitly on the differences between two green crab genotypes (Kanary et al. 2014). The modelling approach used by Kanary et al. (2014) incorporated spatial parameters that allowed them to make predictions about rates of green crab spread. Here, I chose to use a stage-based population matrix model to analyse the population dynamics of the green crab population and its potential changes while exposed to different removal strategies. I explicitly include seasonality, which allowed me to conduct analyses in which removal strategies took place in the summer months, which accurately reflect current mitigation methods.

A stage-based model was considered the most suitable because it functions with a discrete time step, like age-based models, but allows the stage duration to be longer than the model time step, and thus individual organisms may remain in the same life-stage for multiple time steps. While there are a few studies that have designed matrix models specifically for crabs, I am aware of only one publication that successfully employed such an approach to study the sustainable management of the blue crab (*Callinectes sapidus*) (Miller 2001).

The objectives of my study were to use a stage-based population matrix model to simulate the population dynamics of green crabs. I used it to evaluate how each life stage contributes to population growth and reproduction. I then assessed the impact of different

removal strategies on the green crab population. Finally, I applied a fishing parameter to my model to simulate current green crab removal strategies. In the long term the results of this model might be used to aid decisions about harvesting and management for the green crab.

5.3 Methods

5.3.1 Life cycle description and model structure

Green crabs grow through four planktonic zoea stages before metamorphosing into a megalopa, and then settling as a small crab, molting once or twice a year. On the east coast of North America mating occurs in late summer, and megalopa settle about one year after mating (Berrill 1982). In cold water locations like Maine, crabs mate at or after two years old, with an estimated minimum size at sexual maturity of 34mm CW (Berrill 1982).

My model ran on a yearly time step and included seasonal submatrices, representing summer and winter (following Miller 2001 and Caswell 2000) to account for seasonal differences in population dynamics. Such a periodic matrix (i.e. using submatrices) allowed me to explore within year biological detail (i.e. seasons) as well as between year population dynamics. Three stages occur in each season (Figure 5.1). The first stage represents eggs in the summer and young-of-the-year (YOY) in the winter. The second stage represents juvenile crabs in the summer and winter, with the possibility for individuals to stay in the juvenile stage for 1-3 years. The final stage represents sexually-mature adults in the summer and in the winter, with the possibility for individuals to remain in the adult stage for a maximum of six years.

The 3 X 3 transition matrix A_{summer} defines the dynamics affecting summer life history stages (dashed lines in Figure 5.1) whereas the matrix A_{winter} defines the dynamics affecting the winter life history stages (solid lines in Figure 5.1). To project forward from one year to the next, the two season submatrices were combined into an aggregate matrix $A = A_{winter} \times A_{summer}$ following Caswell and Trevisan (1994).

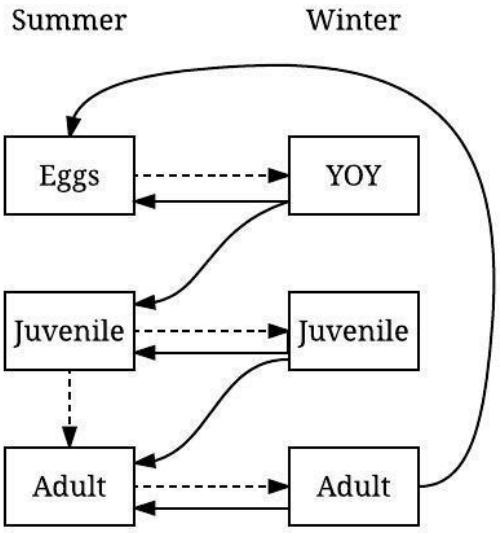


Figure 5.1: Life cycle diagram for green crabs. The life cycle is represented by three stages that occur in summer (left column) and winter (right column). Transitions from summer to winter are shown as dashed lines. Transitions from winter to summer are shown as solid lines.

$$A_{summer} = \begin{bmatrix} G_{11} & 0 & 0 \\ 0 & P_{22} & 0 \\ 0 & G_{32} & P_{33} \end{bmatrix} \qquad A_{summer} = \begin{bmatrix} 0.001159 & 0 & 0 \\ 0 & 0.181851 & 0 \\ 0 & 0.266321 & 0.447199 \end{bmatrix} \quad (1)$$

$$A_{winter} = \begin{bmatrix} 0 & 0 & F_{13} \\ G_{21} & P_{22} & 0 \\ 0 & G_{32} & P_{33} \end{bmatrix} \qquad A_{winter} = \begin{bmatrix} 0 & 0 & 43819.5 \\ 0.225269 & 0.181851 & 0 \\ 0 & 0.266321 & 0.447199 \end{bmatrix} \quad (2)$$

.

Each matrix had three columns because our population has three stage classes. The fertility rates are given on the top row (*F*) in the winter matrix. The survival

probabilities (*G*) represent the survival from one class the next. For example G_{21} is the probability that a young of the year crab will become a juvenile in the winter season. The survival probabilities (*P*) represent the probability that an individual in a given stage will survive and will remain in the same class in the following season. For example P_{22} is the probability that a juvenile will remain a juvenile in the following season. I provide a full explanation of each parameter to clarify transitions for these submatrices below.

5.3.2 Explanation of parameters

Longevity

Berrill (1982) cites maximum longevity of green crab in Maine, USA, as 5-6 years. In other geographic locations where green crab is exotic, maximum longevity estimates vary from 3 to 6 years (Berrill 1982; Baeta et al. 2005; Yamada et al. 2005; Broekhuysen 1936 as cited in Baeta et al. 2005; Naylor 1962 as cited in Baeta et al. 2005). I used longevity estimates to calculate adult survival (described below).

Adult to Adult survival

Natural mortality is difficult to estimate in crustaceans, and has been identified as the most important but least well-estimated parameter in fishery models (Vetter 1988). Edwards (1958) estimated green crab adult survival at 0.64—0.88 from a mark-recapture study in England, but this study only occurred over the span of one month. Another study by Munch-Petersen, Sparre, and Hoffmann (1982) estimated green crab adult survival at 0.07 – 0.95 based on ten separate mark-recapture studies in Copenhagen, but each study only lasted between four and nine days and the authors acknowledged that these

estimates were inaccurate due to the short time span of the experiment and the uncontrolled immigration/emigration.

Natural mortality (across a wide variety of taxa) can be indirectly estimated using a linear regression model (Hoenig 1983) based on longevity, where *M* is the annual natural mortality rate, and t_{max} is the maximum possible age for the species. This equation has been recommended as the simplest and best method for estimating adult mortality in crustaceans (Hewitt 2008).

$$\ln(M) = 1.44 - 0.982 * \ln(t_{max}) \quad (3)$$

Using this method I defined survival as (1 – Mortality), and I estimate that the maximum life span for green crabs was a conservative 5-6 years (Berrill 1982). I calculated annual survival rates to be between 0.273 and 0.131 (for t_{max}=5 or 6 years respectively). In the model, estimates were stochastically drawn from a triangular distribution with a minimum value of 0.131 (t_{max}=6 years), a maximum of 0.273 (t_{max}=5 years), and a most likely value of 0.202 (middle point between these two values). Since the model runs on a 6 month time step, all of these values were raised to the power of 1/2.

Table 5.1: Matrix model parameter definitions. ϕ represents survival, *P* represents the probability of surviving and remaining in the same stage until the next time step, and *G* represents the probability of surviving and growing into the next stage. Fixed values were taken from Monte Carlo simulations (x 1000) of each parameter. Sources: (1) Audet, Miron, and Moriyasu 2008; (2) Berrill 1982; (3) Hoenig 1983; (4) Hewitt and Hoenig 2005; (5) Cooper at al. 2012.

Parameter	Symbol	Estimate for the fixed values model	Distribution in the stochastic model	Source
Number eggs produced/female	F_{adult}	195,833	195,833 ± 83,673	1
Sex ratio	S_r	0.5	--	--
Maximum longevity	t_{max}	5-6 years	--	2
Annual adult survival (based on t_{max}, see sources)	$\phi_{annual\ adult}$	--	Triangle distribution with min = 0.131, most likely value = 0.202, and max = 0.273	3,4
Adult survival (for 6 months)	ϕ_{adult}	0.4472	$(\phi_{annual\ adult})^{1/2}$	--
Probability of remaining a juvenile for another 6 months	P_{juv}	0.4006	Triangle distribution with min = 0, most likely value = 0.5, and max = 0.7071	--
Probability of surviving and remaining in the juvenile stage	P_{22}	0.1819	$P_{juv} * \phi_{adult}$	--
Fecundity	F_{13}	43,819.5	$F_{adult} * S_r * \phi_{adult}$	--
Probability of surviving and growing from the juvenile to adult stage	G_{32}	0.2663	$(1 - P_{juv}) * \phi_{adult}$	--
Probability of surviving and remaining in the adult stage	P_{33}	0.4472	ϕ_{adult}	--
Egg to YOY survival	G_{11}	0.00116	Exponential distribution with a mean of 0.001159	5
YOY to juvenile survival	G_{21}	0.2253	Uniform float distribution with a min = 0.001159, and a max = 0.447199	--
Fishing parameter for adults	f	0.125 – 1	Range of values in place of being able to estimate fishing pressure via trapping	--
Fishing parameter for juveniles	f'	0.0084 – 0.0670	$0.067 * f$	--
Probability of surviving and remaining in the adult stage with fishing	$P(f)_{33}$	Range of values	$\phi_{adult} - f$	--
Probability of surviving and remaining in the juvenile stage with fishing	$P(f')_{22}$	Range of values	$P_{juv} * (\phi_{adult} - f')$	--
Probability of surviving and growing from the juvenile to adult stage with fishing	$G(f')_{32}$	Range of values	$(1 - P_{juv}) * (\phi_{adult} - f')$	--

Fecundity

Fecundity (*F*) represented the number of eggs produced by female adult crabs, assuming crab survival. I included fecundity in the winter matrix because the crabs release their eggs during this season (Audet, Miron, and Moriyasu 2008). Fecundity estimates were stochastically drawn from a truncated normal distribution with a mean of 195,833 and a standard deviation of 83,673 (Audet, Miron, and Moriyasu 2008). This distribution was truncated at 0 to account for the chance that females may not produce eggs and to prevent negative values, and truncated also to 450,000, which was the maximum number of eggs recorded in the literature Audet, Miron, and Moriyasu (2008). This value was multiplied by 0.5 to account for the sex ratio, which was assumed to be equal, and multiplied by the adult survival for 6 months (ϕ_{adult}). Natural mortality was included in this transition following Miller (2001), and Kissel et al. (2014).

Egg to Young-of-the-year (YOY) Survival

Estimates for egg to young-of-year (YOY) survival were stochastically drawn from an exponential distribution with a mean of 0.001159 (Cooper et al. 2012). This data was taken from Figure 2 of Cooper et al. (2012), which reported field observations of YOY (named 'group 0' by Cooper) settlement rates (defined as 'the probability that an egg will survive through the larval stage and settle on suitable habitat'). YOY were defined as crabs which had a carapace width of more than 10mm (Berrill 1982).

YOY to Juvenile Survival

I am not aware of any studies detailing survival of YOY to the juvenile stage. Following the approach used by Miller (2001) I anticipated that the survival rate would decline linearly from the egg to YOY survival rate to the background adult mortality. I used a uniform float distribution with a minimum of 0.00116 (G_{11}), and a maximum of 0.0447 (ϕ_{adult}), which gives a mean of 0.2253. This estimate also concurs with YOY to juvenile survival rates reported in Cooper et al. (2012).

Juvenile to Juvenile Survival

The probability that a juvenile remains and survives in the juvenile stage for another year was broken down into two parts: annual adult survival, and the estimated probability that a juvenile will remain in the juvenile stage until the next time step (6 months). Annual adult survival estimates were estimated as described above (ϕ_{adult}).

For colder water locations in the green crab's invaded range on the east coast of North America, age of maturity was estimated to be between 2 and 3 years, which corresponds to remaining in the juvenile stage for 1-2 years (Berrill 1982). Based on this, estimates that a juvenile will remain in the juvenile stage for another year were stochastically drawn from a triangle distribution with a minimum value of 0, a most likely value of 0.5, and a maximum value of 0.7071. The minimum value (zero) represents the probability that all individuals would transition to the adult stage after one year (probability of remaining in the juvenile stage for another year = 0). If individuals remained in the juvenile stage for two years, I assumed that half of all juveniles would transition to the adult stage each year. This equateed to a 6 monthly probability of $0.5^{1/2}$.

The most likely value was the middle value of 0.25, raised to ½ to account for the 6 month model to reach a value of 0.5. These values were derived from the percentage of the juvenile population that would remain in the juvenile stage from one 6 month time step to another if juveniles remain in the juvenile stage for 1-2 years respectively.

Juvenile to Adult survival

Juvenile to adult survival was estimated by multiplying the annual adult survival by $(1 - P_{juv})$.

Fishing model

I added in a fishing parameter (f) into my model in order to investigate the impact of fishing pressure (Table 5.1). I used two simple methods to mimic fishing pressure, because no quantitative data was available to estimate fishing mortality rates. First, I used a very simple approach in which I selected a range of values from 0.125 to 1 for the adult fishing parameter to represent low to high mortality rates (or removal). The lowest value was much lower than natural mortality, while the highest value was double the natural mortality. Fishing mortality was applied to both adult and juvenile stages in the model.

Secondly, I attempted to mimic a fishing pressure that would be similar to the combined use of three types of trapping gear (fukui traps, fyke nets, and minnow traps) and that would represent the traps typically used in green crab removal efforts. To estimate fishing pressure on adult and juvenile crabs separately I used trapping data from a project monitoring green crabs at two locations on the east coast of Prince Edward Island, Canada (Quijón et al. unpublished data). I assumed that juveniles are smaller than

35mm CW (Berrill 1982). These data showed that for every adult caught, 0.067 juveniles were caught. Since I did not have access to intensive trapping data, I tested a range of values that would represent low to high fishing pressure, with juvenile pressure (f') being 0.067 that of adult pressure (f).

5.3.3 Model Analysis

To investigate the contribution of each life stage to the overall population growth of green crab, I conducted several analyses on the stage-based population matrix model in Excel ® using the add-on Poptools (following Barbour et al. 2011). Initially I used fixed values in the model, and then conducted the same analyses using stochastic values.

First, I conducted a base projection of the model to predict the annual population growth rate (λ) in the absence of harvesting. Lamba was the dominant eigenvalue of the matrix and values of λ exceeding 1 indicated a growing population, whereas values of less than 1 indicated a declining population. I also calculated the stable stage distributions and reproductive contributions for both the summer and winter matrices.

Next, both sensitivity and elasticity analyses were calculated for each seasonal submatrix individually, following other studies with period matrix models (e.g. Mertens, Van Den Bosch, and Heesterbeek 2002; Westerman et al. 2005). I do not report sensitivities and elasticities of the aggregate matrix because they do not have a clear interpretation (Caswell and Trevisan 1994). Sensitivities show the impact of absolute changes in each vital rate on the population growth. All the parameters (transition probabilities) were constrained between zero and one, except for fecundity, and so it was also helpful to report elasticities. Elasticities measured the proportional contribution of

each vital rate on population growth, and sum to one in an individual matrix. Elasticities depended on a stable stage distribution and should be compared qualitatively (Miller 2001).

Following the analyses described above, I systematically varied one parameter at a time to determine the impact of a particular transition probability on the annual population growth rate (λ). Next, I varied two parameters at the same time to examine the impacts on λ. This analysis showed the magnitude of change required for different combinations of parameters in order to make the population growth rate (λ) drop below 1, indicating a declining population growth rate. Finally, I included the fishing parameter (following Miller 2001) that removed a proportion of adults and juveniles per year as part of a theoretical removal program.

5.4 Results

5.4.1 Base Projection

An initial projection of the model, using the fixed values of all parameters based on values from the literature (Table 5.1), predicted that the crab population would increase in number each year. The value of λ=1.9010 indicates an increase of approximately 90% per year (Table 5.2). When this same analysis was run using stochastic life-history values, the model predicted that the green crab population could increase by about 43% per year (λ=1.43) (Table 5.2).

Table 5.2: Population growth rate (λ) estimates for the individual summer and winter matrices, as well as the aggregate (annual) matrix for both the fixed values and the stochastic values model.

	Population growth rate (λ)	
	Fixed values model	Stochastic values model
Summer Matrix	0.4472	0.2692
Winter Matrix	14.0124	13.0205
Aggregate Matrix	1.9010	1.4351

The stable stage structure of the population differed for the summer and winter matrices (Table 5.3). The winter matrix was dominated by the eggs to YOY stage, which reflects the high fecundity of green crabs. The summer matrix was dominated by the adult stage, which is likely a more accurate representation of the expected stage distribution found in estuaries. The stable stage of eggs and juveniles was 0 most likely because the adults do not reproduce during the summer phase of the model.

The reproductive value, which measures the contribution of a given life stage to the future population growth rate, differed for the summer and winter matrices (Table 5.3). The adult stage had the greatest contribution to the reproductive output in the winter matrix, which was reflective of the high number of eggs that adult females release in the spring. In the summer matrix, the juvenile stage had the highest contribution to the reproductive output, which represents the juveniles that grow to become adults in the winter.

Table 5.3: Stable stage distributions and the reproductive contribution values for the summer and winter matrices calculated from both the fixed values and stochastic values models.

	Life stages	Stable stage		Reproductive values	
		Fixed values model	Stochastic values model	Fixed values model	Stochastic values model
Summer Matrix	Eggs	0	0	0	0
	Juveniles	0	0	0.5501	0.8094
	Adults	1	1	0.4991	0.1906
Winter Matrix	YOY	0.9837	0.9837	0.0003	0.0003
	Juveniles	0.01607	0.0160	0.0189	0.0227
	Adults	0.00037	0.0003	0.9808	0.9770

5.4.2 Model sensitivity and elasticity

The sensitivities of the summer and winter matrices differed. For the summer matrix, adult survival was the most sensitive and elastic vital rate (Table 5.4). I conducted a post-hoc assessment to gain insight into this sensitivity result. To do this I tested a range of values for the adult survival parameter, and I then recorded the resulting population growth rate (λ) for each individual matrix (summer and winter), and for the aggregate matrix using both the fixed values model, and the stochastic values model (Table 5.5). This analysis showed that the adult survival parameter had a large influence on the summer matrix λ, but no influence on the winter matrix λ. Since the winter matrix has a much larger λ value than the summer matrix, the winter matrix has a comparatively much larger impact on the overall (annual) population growth rate (Table 5.2).

Table 5.4: Sensitivity and elasticity of the summer and winter matrix for both the fixed values and stochastic values model.

	Parameter	Fixed values model		Stochastic values model	
		Sensitivity	Elasticity	Sensitivity	Elasticity
Summer Matrix	Eggs to YOY	0	0	0	0
	Juvenile to juvenile	0	0	0.3970	0.4050
	Juvenile to adult	0	0	0	0
	Adult to adult	1	1	0.6030	0.5950
Winter Matrix	Fecundity	0.0001	0.328	0.0001	0.3270
	YOY to Juvenile	20.4204	0.3283	30.1994	0.3270
	Juvenile to juvenile	0.3326	0.0043	0.3324	0.0054
	Juvenile to adult	17.2727	0.3282	16.5794	0.3270
	Adult to adult	0.3391	0.0108	0.3405	0.0135

Table 5.5: Post-hoc assessment of the summer sensitivity and elasticity. Results show the population growth rate values (for the individual summer and winter matrices, and for the aggregate matrix) for a range of values for the adult survival parameter (changed in the summer matrix only). Values were recorded for both the fixed values model, and the stochastic values model.

	Adult-adult parameter	Summer matrix λ	Winter matrix λ	Aggregate matrix λ
Fixed model values	0.1000	0.1800	14.0124	1.7900
	0.2000	0.2000	14.0124	1.8000
	0.4472	0.4472	14.0124	1.9000
	0.6000	0.6000	14.0124	1.9000
	0.8000	0.8000	14.0124	2.000
Stochastic model values	0.1000	0.1805	12.9430	1.2553
	0.2000	0.2197	12.7065	1.3894
	0.4472	0.4472	12.5827	1.4179
	0.6000	0.6000	12.5452	1.6753
	0.8000	0.8000	13.0404	1.6136

For the winter matrix, the YOY to juvenile transition stage was the most sensitive, followed by the juvenile to adult transition stage (Table 5.4). The highest elasticity value was shared equally by three stages: YOY to juvenile stage, the juvenile to adult stage, and the fecundity. Since elasticities are additive and should be interpreted qualitatively, this indicates that the population will respond most to changes in those rates. Thus

population growth in the winter was most dependent on the production of eggs and on the transition of the early life stages (young of the year and juveniles, juveniles to adults).

5.4.3 The effect of parameter variation on population growth

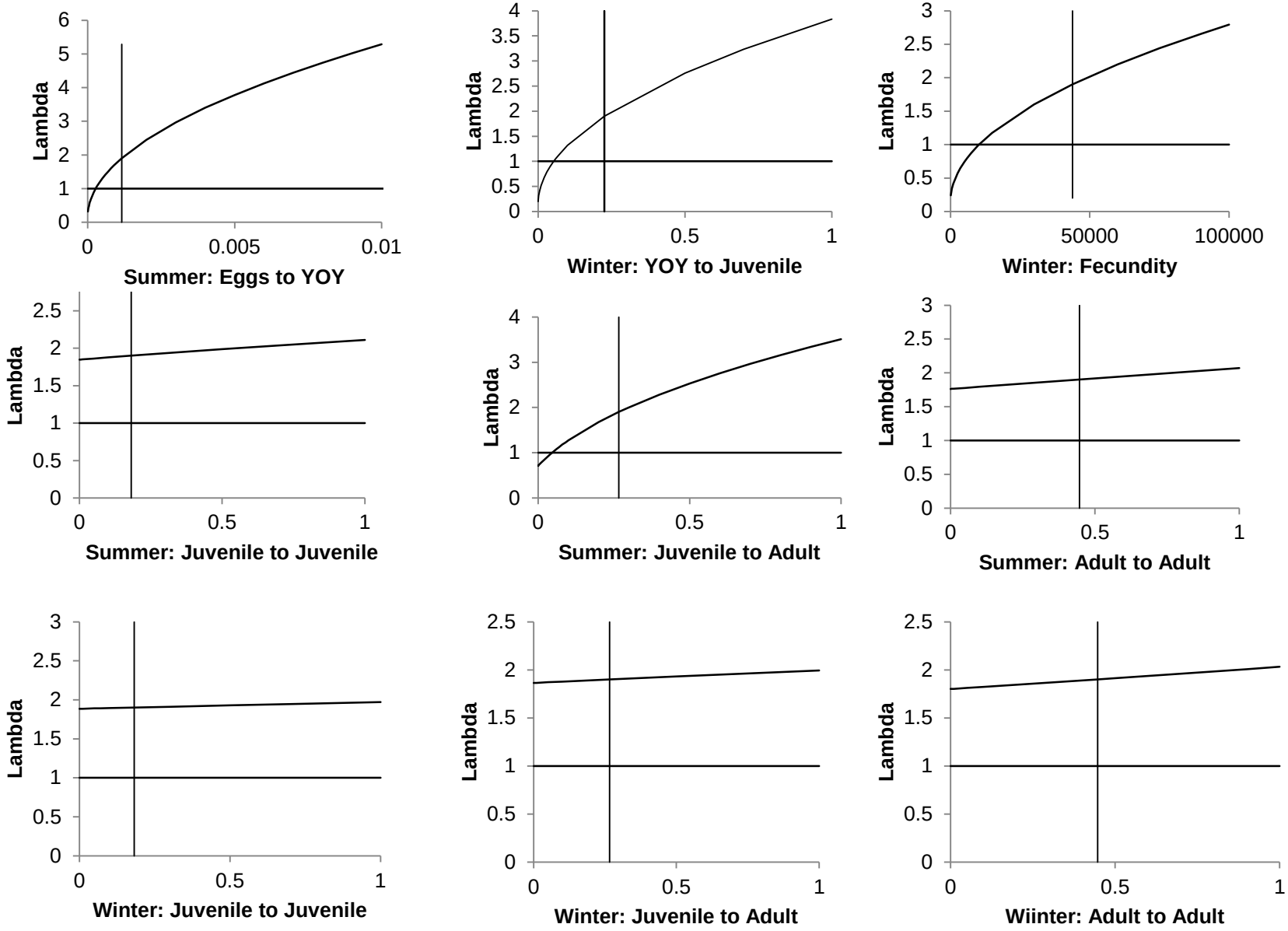
Using fixed values (shown in Table 5.1) I varied one parameter at a time in the seasonal matrices (A_{summer} or A_{winter}) to determine the effects on the population growth (λ) in the amalgamated matrix (A). Most of the parameters (adult survival, juvenile survival in summer and in winter as well as juvenile transition to adults in the winter) had very little impact on λ, with values remaining between 1.5 and 2.5, even when the specific individual parameter was set to zero (i.e. no survival for the transition) (Fig. 5.2). This indicates that for all values tested, the population continued to increase yearly.

Four parameters, (eggs to YOY in the summer, juvenile to adult in the summer, YOY to juvenile in the winter, and fecundity) did have an influence on the growth rate of the population. For all of these parameters, λ dropped below one (indicating a declining population) for very small values.

Next, I varied two parameters at the same time to examine the impacts on λ, focussing on the three parameters that had a substantial effect on lambda (revealed in the tests described above) that we could feasibly influence in the field. I did not include fecundity because I am unaware of any methods that could influence the fecundity of a crab in the field. This analysis enabled identification of the parameter space where $\lambda < 1$, which is when the population is declining. My results showed that a substantial change in at least one of these parameters was required to result in population decline (Fig. 5.3).

These analyses were also completed using the stochastic model, which showed the same general trends as the fixed values model (Fig. 5.4, Fig. 5.5).

Figure 5.2: Impact of a range of values for each parameter (using the fixed values model) on the population growth rate (lambda). Values for lambda above one indicate an increasing population, whereas values below one indicate a decline population growth rate.



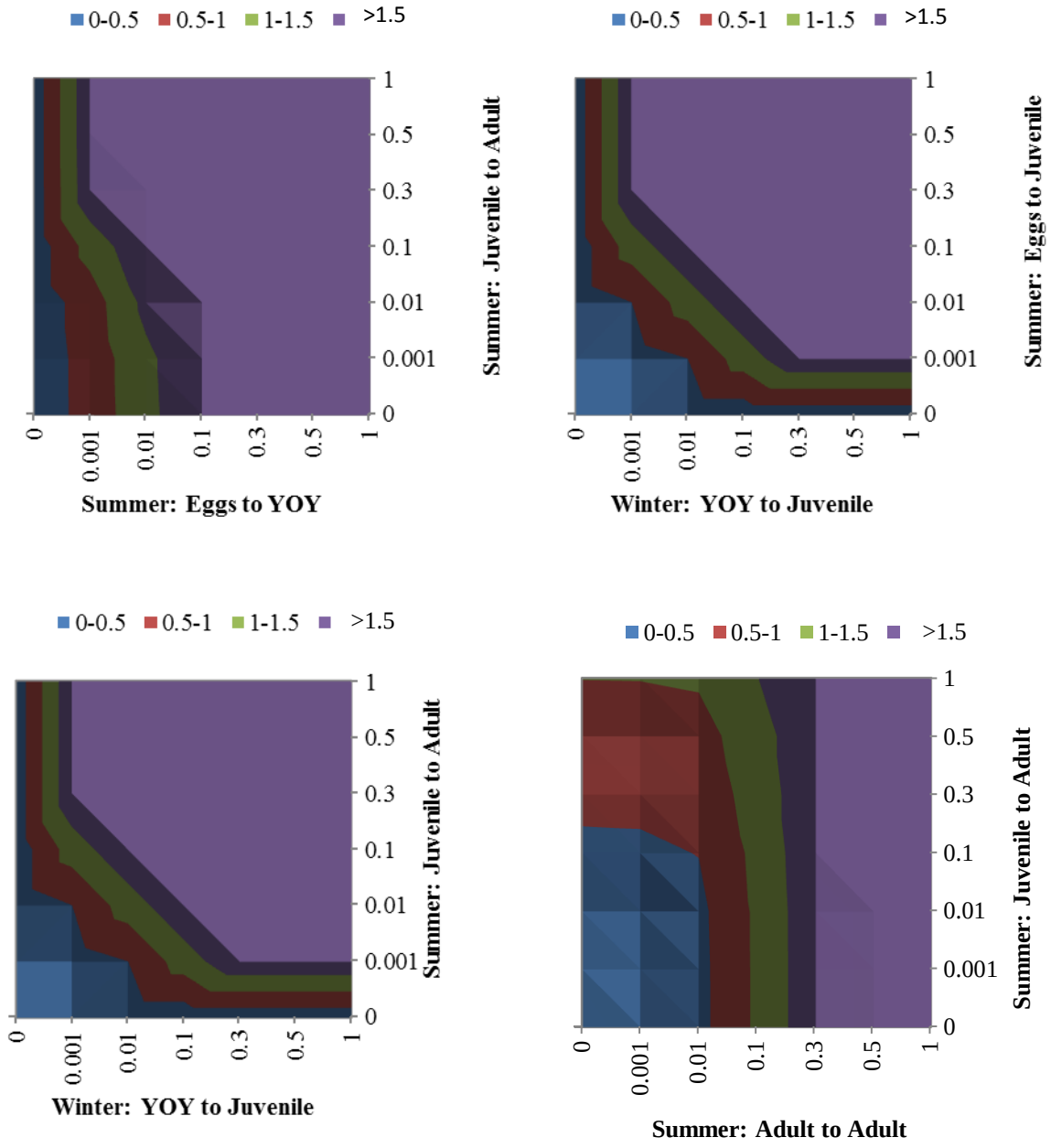
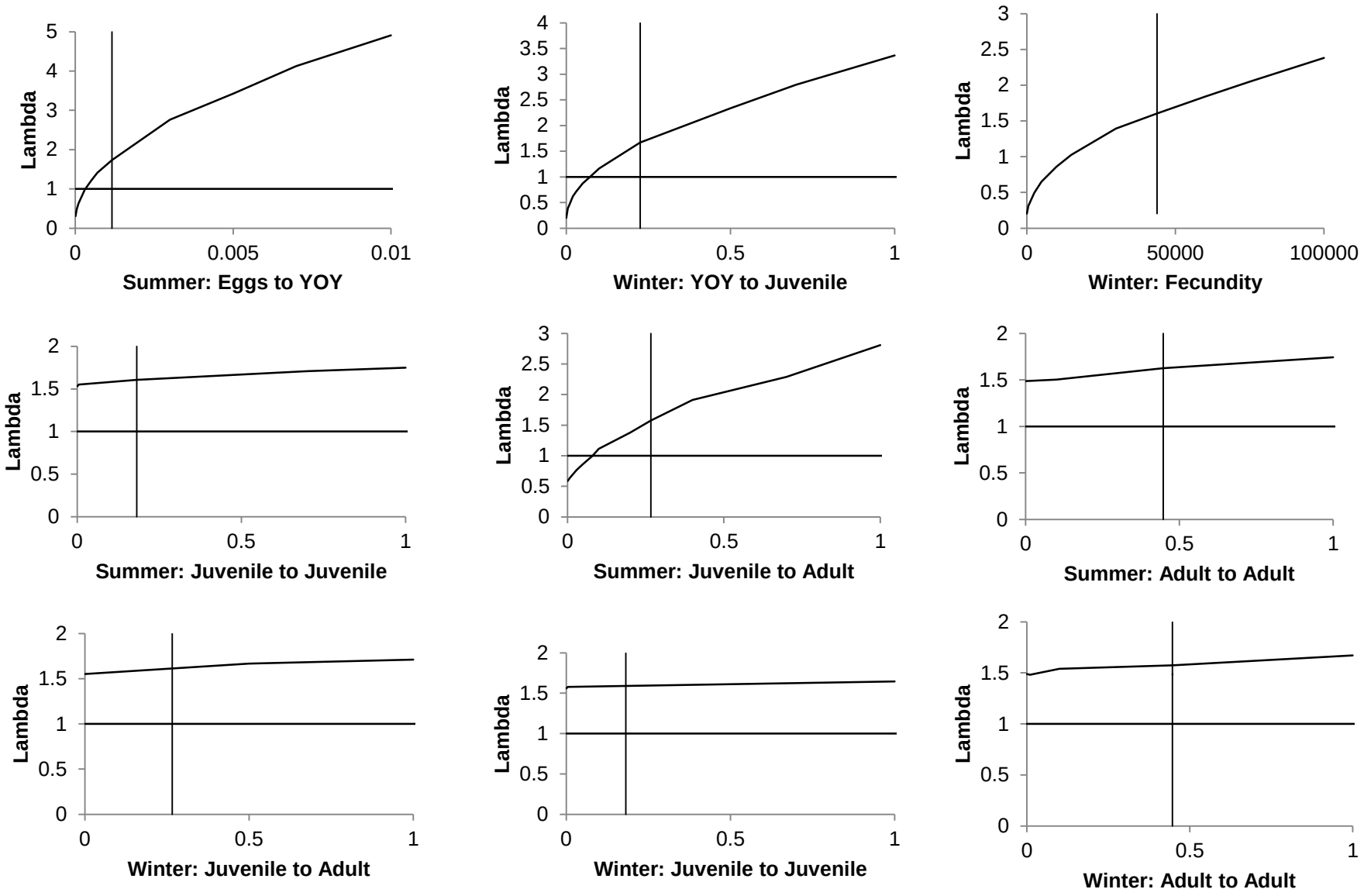


Figure 5.3: Impact of changing two parameters (testing a range of values using the fixed value model) on the population growth rate (λ), represented by the different colours. λ values above one indicate an increasing population growth rate, whereas values below one indicate a decreasing population growth rate.

Figure 5.4: Impact of a range of values for each parameter (using the stochastic values model) on the population growth rate (lambda). Values for lambda above one indicate an increasing population, whereas values below one indicate a decline population growth rate.



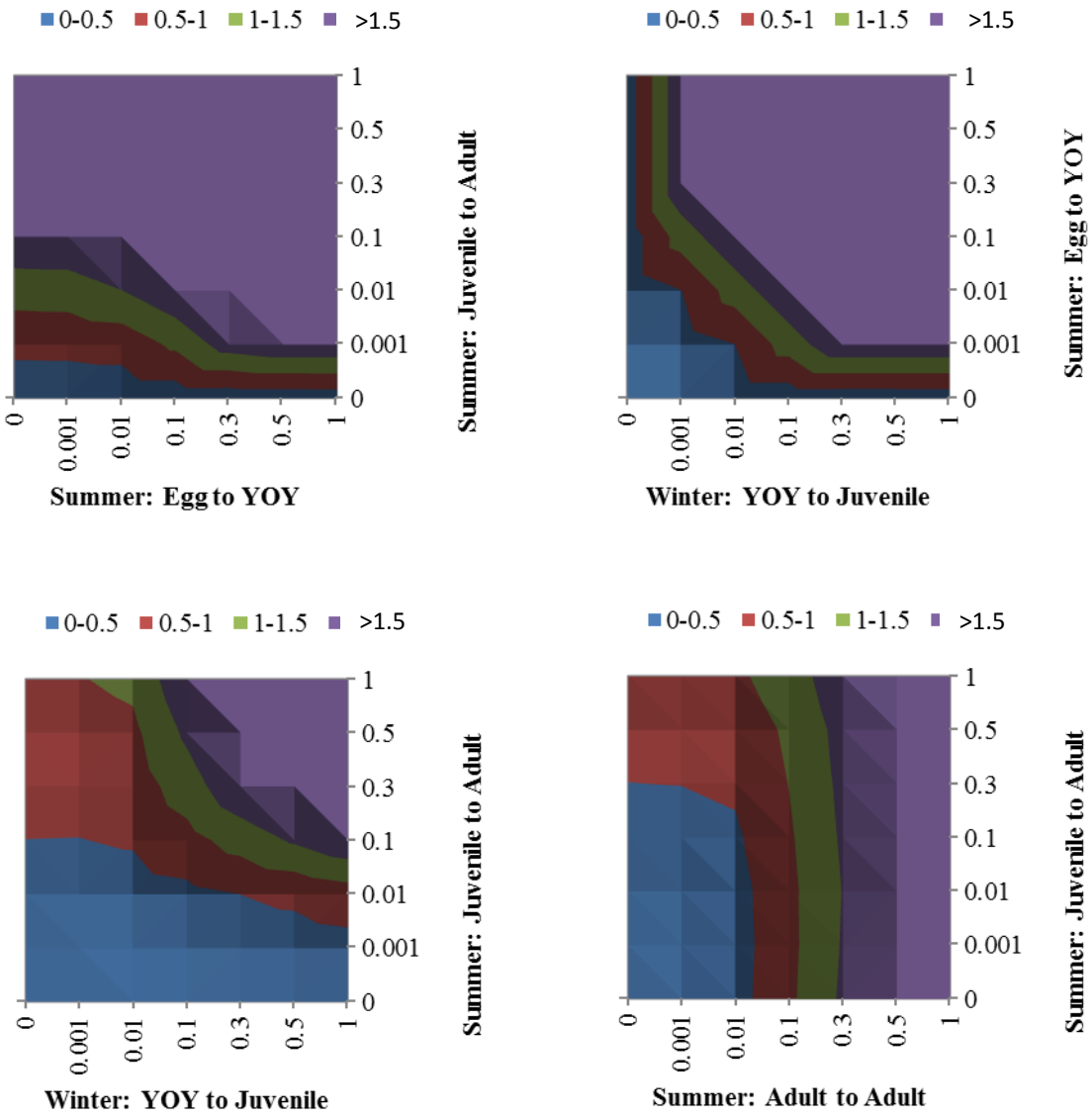


Figure 5.5: Impact of changing two parameters (testing a range of values using the stochastic values model) on the population growth rate (λ), represented by the different colours. λ values above one indicate an increasing population growth rate, whereas values below one indicate a decreasing population growth rate.

5.4.4 Fishing Model

When I used the fishing parameter based on the adult : juvenile catch ratio estimated from the trapping data (using fukui traps, fyke nets, and minnow traps), the analysis showed that the population growth rate (λ) did not decline below 1, even when fishing pressure was set higher than the natural adult mortality (equivalent to setting adult survival to zero) (Table 5.6). When I used the fishing parameter based on an equal adult : juvenile catch ratio, I found that the population growth rate did decline below 1, indicating a declining population.

Table 5.6: Influence of a range of values for fishing pressure on the population growth rate of the aggregate (annual) matrix. *f* represents the fishing pressure for adults, and *f'* represents the fishing pressure on juveniles. λ values below 1 indicate a decline in the population growth rate, whereas λ values above 1 indicate an increase in the population growth rate.

	f	***f'***	**Aggregate matrix λ**
Fishing parameter based on catching an adult: juvenile ratio that is based on trapping data	0.125	0.0084	1.8503
	0.25	0.0168	1.7948
	0.375	0.0251	1.7391
	0.5	0.0335	1.6831
	0.625	0.0419	1.6268
	0.75	0.0586	1.5701
	0.875	0.0586	1.5130
	1	0.0670	1.4554
Fishing parameter based on catching an equal ratio of adults: juveniles	0.125	0.125	1.5978
	0.25	0.25	1.2312
	0.325	0.325	0.9578
	0.35	0.35	0.8501
	0.375	0.375	0.7287
	0.4	0.4	0.5853
	0.425	0.425	0.3979

5.5 Discussion

Population matrix models are useful tools for investigating population dynamics, especially when there are large gaps in knowledge about particular life stages of a species. They can play an important role, for example in conserving at-risk species (e.g. Crouse and Crowder 1987), calculating the harvest limit of commercially important species (e.g. Miller 2001), or attempting to reduce the population density of invasive species (e.g. Govindarajulu, Altwegg, and Anholt 2005). This chapter represents a first attempt to use a matrix model to investigate how removal scenarios may affect green crab population as a whole. Population matrix models have rarely been applied to crustaceans (but see Miller 2001), and this study is the first to use matrix models to investigate the green crab population dynamics.

Choosing the level of detail to include in models is one of the fundamental decisions population biologists must make when creating a model. My model estimated that the green crab population can increase by approximately 90% per year (λ=1.9) using fixed values gathered from the literature, and by 43% per year when population stochasticity was included. Both estimates indicate an increasing green crab population which is in line with surveys in North America that show increasing range expansion and increasing abundance (Cohen, Carlton, and Fountain 1995; Jamieson et al. 1998; Audet et al. 2003; Yamada and Randall 2006; DFO 2011). While the rate of population growth may seem high, the values of between 43 and 90% are most influenced by the model parameters that control the fecundity (production of eggs), as well as the survival of the eggs and the young of the year. These parameters were the most difficult to estimate. The parameter values were based on mean values from field and laboratory experiments. In

reality, under some field conditions, it is possible that population growth rate would be lower than estimated here if environmental conditions are on average less favourable for reproduction and larval survival.

My sensitivity and elasticity analyses showed that adult survival was the most sensitive and elastic parameter in the summer matrix. This indicates that a fishing strategy that aims to decrease adult survival in the summer (which is the season and life stage that current removal programs focus on) would have the greatest impact on decreasing the population growth rate in the summer. However, the value of λ in the winter matrix was over 30 times greater than the summer matrix λ value (Table 5.2), and thus has a much greater influence on the overall (annual) population growth. This means that although decreasing the adult survival in the summer may cause population declines in the summer, the high fecundity of these crabs, and the survival rate of larvae (represented as the most sensitive and elastic parameter in the winter matrix) dominate the annual population growth. Data from multi-year trapping programs in Newfoundland has found similar results. Therriault and Duncombe (2016) conducted trapping from 2010-2015 in Pipestem Inlet and found that catch per unit effort (CPUE) decreased over the duration of a summer season. However, this study found that CPUE was similar between yearly trapping events. This means that the population declined in the summer as a result of fishing, yet recovered over the winter months. Similarly, Matheson et al. (2016) conducted large-scale trapping in Placentia Bay from 2014-2016, and found that catch rate decreased by up to 75% over the course of the season, but that total abundance of crabs in the population were similar between years.

A close inspection of the model showed that some parameters, including adult survival, had little impact on the population growth rate. This is interesting because trapping programs are often targeted towards catching adults (via use of fukui traps), and this result from my model suggests that even if all adults are removed from a population, the population may still be able to sustain itself. The population is still able to grow because there are enough of the other life stages to feed the population growth rate. For example, when the specific individual parameter of adult survival was set to zero, there were still high enough numbers of juveniles that become adults and reproduce quickly enough before they die to sustain the population. Many removal programs have resulted in little-to-no declines in green crab year-to-year abundances, in agreement with my model results, suggesting self-sustaining populations (Walton 2000; Klassen and Locke 2007; Duncombe 2014). However, some removal programs have recorded a decline in green crab average carapace width between years. A consequence of this is a population comprising a higher proportion of small green crabs, vulnerable to native predators like larger crustaceans and shorebirds (DFO 2011, Matheson et al. 2016, Therriault and Duncombe 2016). In the long term, a program that results in smaller size crabs may promote predation and further population decline.

In my model, there were only four parameters that could promote a decline in the population growth rate. Interestingly, all these are parameters that involve transition of one stage to the next. These parameters are effectively feeding the life stages of the model (compared to the parameters that influence the probability of remaining in the same life stage in the next time step). In practice, it is difficult and likely unfeasible to target most of these life-history stages. Planktonic stages that are released into the water

are impossible to target, and I have found it very difficult to locate YOY green crabs in the Prince Edward Island region. The only stage that has an effect on λ that could be practically useful is fecundity. Removal programs could target ovigerous females by increasing trapping intensity during the season that females are carrying eggs, and my model shows that this could potentially have a positive impact on reducing the population.

When I included fishing in my model by using a mortality parameter that was based on the adult:juvenile catch ratio estimated from the trapping data (using fukui traps, fyke nets, and minnow traps), my model showed that the population growth rate (λ) did not decline below 1, even at very intensive trapping levels. I used this fishing parameter as a way to more realistically assess whether trapping in the summer months could impact the green crab population growth rate. The fishing parameter (*f*) does not have a 'real world' meaning, but suggests that using the trapping gear that is currently being used to catch green crabs, even very intensive trapping programs will be unable to reduce the population growth rate. The feasibility of establishing a soft-shell green crab product similar to the Moleche industry in Venice, Italy, is currently being investigated in the Canadian Maritimes (St-Hilaire et al. 2016; Poirier et al. 2016). My analysis concurs with the results of a previous green crab population model (Kanary et al. 2014) which suggest that a fishery is likely to be sustainable, and that high levels of adult harvesting can be tolerated without creating a situation where green crabs are easily overfished.

When I used the fishing parameter based on an equal adult:juvenile catch ratio, I found that the population growth rate did decline below 1, indicating a declining population. This result suggests that if new trapping gear or techniques could be

developed that are capable of catching high numbers of juveniles, in addition to current trapping gear that catch mostly adults, then intensive trapping could be capable of decreasing the population growth rate.

Limitations to my modelling approach must be considered. The results of the model indicate that the green crab population is increasing, and that harvesting adults alone (as is the current practice) will not be sufficient to reduce green crab populations. However, the environmental conditions of a specific area are important to keep in mind when considering the impact of a removal program. Cosham, Beazley, and McCarthy (2016) summarize the habitat selection of green crabs at various spatial scales, and emphasize that habitat variations have a big effect on the ability of a simple model to accurately predict local green crab population responses. For example, Barbour et al. (2011) created a matrix model for lionfish that suggested that removal programs might be successful in small, localized areas where high exploitation rates could be achieved, whereas removals would be unlikely to be successful in large areas with higher immigration rates.

It is also important to consider the time since invasion in a discussion about removal programs for invasive species. The classic model for the early stage of invasion is exponential growth (Crook et al. 1999), followed by a less steep slope of population increase. This means that the success of a removal program in a particular area may also depend on what stage of growth the population is in, and how recently green crabs invaded that region. In Prince Edward Island, for example, green crabs were first confirmed in 1997, so they have only been here for approximately 20 years, and may still be in an exponential growth stage (green crabs are spreading and increasing in numbers

on the west end of the island indicating exponential population growth). Additionally, green crab populations are known to exhibit strong yearly variations in abundance due to warm winter temperatures (Gillespie et al. 2015), or in response to El Niño events (Yamada and Randall 2006), which would also have an impact on the success of a removal program.

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CHAPTER 6

Summary of results and future research recommendations

6.1 Summary of results

The research reported in this thesis aimed to address critical gaps in knowledge specific to three main topics: (1) how habitat affects green crab predation rates of native mud crabs (*Dyspanopeus sayi*), (2) how habitat affects green crab cannibalism rates on juvenile-stage crabs, and (3) population dynamics with a first attempt at developing a green crab population matrix model.

The first research section of this thesis (Chapter 3) investigated spatial associations between the native mud crabs and invasive green crabs, followed by an exploration of the effect of habitat on the predator-prey interactions between these two species. Long-term observational beach-seine data collected from the southern Gulf of St. Lawrence found that there was a negative association between mud crabs and green crabs in this area. I conducted laboratory experiments examining one of the possible causes of this negative relationship: predator-prey interactions between these two species, assessing simultaneously how this was influenced by the habitat in which those interactions took place. I found that green crab predators consumed almost twice as many mud crabs compared with juvenile green crab prey in the two less-structured habitats, but found also that those predation rates were similar in the most structured habitat. Predation rates on mud crabs were significantly affected by habitat type, whereas predation on juvenile green crabs was unaffected. The results suggest that as green crabs continue to invade areas dominated by mud crabs, they may threaten the sustainability of this native species.

The next research section (Chapter 4) built on the previous chapter and examined how habitat affects green crab predation rates. However, this research focused exclusively on green crab cannibalism by adults on juveniles. I used laboratory experiments, similar to the ones conducted in Chapter 3, but I used habitat types that represented a wider range of structural complexity. In the previous chapter, green crab predation rates on juvenile green crabs were unaffected by the habitat type. However, with the addition of a broader array of habitat types in this chapter, I found evidence that green crab cannibalism rates decreased with increasing habitat complexity. This chapter also included field experiments using three habitat types. These experiments found a similar trend between cannibalism rates and habitat type as the laboratory experiments, although the differences were not significant. The combined laboratory and field results from this research support the idea that complex habitats have the potential to mediate predator-prey interactions, even though more studies should be conducted on the specific factors associated to habitat complexity that could explain these results.

The third topic addressed in this thesis examined the population dynamics of green crabs. I gathered all the available information about green crab life stages to produce a comprehensive summary of green crab population information (compiled in Chapter 2). I summarized information about fecundity, survival rates between life stages, longevity, and generation time, identifying gaps in knowledge and directions for future research. I found that more information is required to determine the temperature and length of time required for green crabs to be able to have two broods per season. I also suggested that more studies examine the survival rates and abiotic tolerances of larval stages in the laboratory to further clarify the range of variation in the data available.

Finally, I call for a clearer method for estimating longevity in decapods in order to produce more accurate estimates and consistency across geographical locations. As the current best method for estimating adult mortality is based on longevity, I advocate that this is a particularly important parameter to focus further research.

The information compiled in Chapter 2 was applied in the final data chapter of this thesis (Chapter 5) to build a relatively simple stage-based population matrix model for green crabs. This model ran on a yearly time step, and included seasonal submatrices representing summer and winter, with three life stages in each season. The model estimated that the green crab population may be increasing by approximately 43% (when population stochasticity was included). The outcome of this model also suggested that even if adult survival is set to zero (representing intensive trapping and effective removal of adults), the theoretical population was still able to grow because numbers in the other life stages were abundant enough to feed and maintain the population growth rate. Although this is only a first attempt to model the potential consequences of a highly effective removal program, these results are in agreement with the results of several actual removal programs that have shown little-to-no declines in green crab year-to-year abundances (Walton 2000; Klassen and Locke 2007; Duncombe 2014, Matheson et al. 2016; Therriault and Duncombe 2016).

6.1 Suggestions for future research

Green crabs continue to spread regionally and globally, and continue to cause ecological and economic impacts on different ecosystem components. Considerably more

research still needs to be done, and based on the studies conducted in this thesis, I have several suggestions for directions of future research.

The predation experiments presented in this thesis took place in relatively small enclosures with a limited number of predators and prey. A logical next-step is to do similar experiments with different numbers of predators and prey. There are several questions that could be examined. Is green crab foraging affected by the presence of a conspecific or a heterospecific predator such as the rock crab (*Cancer irroratus*) or American lobster (*Homarus americanus*)? How are predation rates affected by prey density, and how do these change with enclosure size? Isolating and examining these factors in further experiments would more accurately explain predator-prey interactions and reflect particular natural conditions.

Building on the idea of making the enclosure experiments more realistic, it would also be interesting to include different types of habitats. Most notably missing from the experiments in this thesis are eelgrass bed (*Zostera marina*) mimics. Green crabs are known to uproot and graze on eelgrass beds, and have been associated with the declines of eelgrass beds in many regions (Davis et al. 1998; Malyshev and Quijón 2011; Garbary et al. 2014). Therefore, conducting enclosure experiments in eelgrass bed habitats would be an obvious next choice because of their common use by this species, and because it may represent a habitat where feeding rates change more drastically than those associated to shellfish beds. Additionally, natural well-structured habitats could be added to the field enclosure experiments. For example, cage enclosures could be conducted on top of live mussel and oyster beds to get a more realistic understanding of predation rates in that habitat type. However, it would be impossible to control for alternative prey sources

available in a live bivalve bed in the field, so the presence of confounding factors would be unavoidable.

Interestingly, the mud crab (*D. sayi*) native to eastern North America has invaded parts of the Adriatic and Mediterranean Seas in Europe, and is causing concern to shellfish farmers (Mistri 2004). In these locations, a green crab congener, *Carcinus aestuarii*, a very similar but genetically distinct species to *Carcinus maenas*, is a native species. In would be very interesting to examine the spatial associations, and predator-prey interactions between these two species in a geographical location where the mud crab is the invasive species, rather than the native species. These types of comparative studies allows for rigorous testing of the hypotheses regarding the interactions between two species, and how geographic location (and the biotic and abiotic factors associated with the change in location) could affect those interactions (Hierro, Maron, and Callaway 2004).

With regards to green crab population biology and population modelling, there is much to be done. Even for a species so broadly studied as the green crab, the literature review provided in this thesis outlines many knowledge gaps in the population biology of this species. Therefore, there are also many possible venues for population modelling of green crabs as more accurate data becomes available, or different modelling techniques are applied to this species. In this thesis, I developed the first stage-structured matrix model for green crabs, but this model is admittedly simple, and could be further developed to include more complex information (e.g. environmental conditions specific to a certain location) to more accurately reflect reality. In addition, validation exercises could also be carried out on the model proposed. For example, we could test some of the

estimates and predictions provided by this model by using real data from a removal program, something that was impossible during the time this thesis was prepared and escaped its scope. Additionally, the model may be used to predict how much sustained effort (in number of years) would be required to alter green crab populations in a particular area. This may serve two purposes: first, to identify how much effort is required to keep green crab populations under control (below a certain level). Second, to identify the level of harvesting that would reduce a population below the level required to sustain a fishery for green crab, assuming that is ever undertaken for commercial purposes.

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